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Foraging behavior of free-ranging Weddell seals (*Leptonychotes weddellii*) in the Antarctic fast-ice environment

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Dedication

To my parents, Ted and Shirley Madden, who have supported me on every decision and whose faith in me is unwavering. Without their continued support and encouragement, this would not have been possible.

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Foraging behavior of free-ranging Weddell seals (*Leptonychotes weddellii*) in the Antarctic fast-ice environment

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Detailed information on diet and foraging behavior is necessary for understanding predator-prey interactions and food-web dynamics. The primary objective of this dissertation was to gain a more complete understanding of the natural foraging behavior of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica using a video data recorder to document the seal's three-dimensional movements and encounters with prey. Seals exhibited a variety of dive types that could be sorted into five groups based on 18 dive descriptors. Three of these groups (deep aerobic, deep anaerobic, and shallow aerobic) were identified as foraging dives, the frequency of which varied with bathymetry. Deep aerobic foraging dives were similar in depth and duration to foraging dives in previous studies and were more common at offshore breathing holes. However, differences occurred between offshore free-ranging and isolated-hole dives in the behaviors involving descent and the frequency of certain behavioral transitions. These differences were responses by the seals to variations in prey abundance, rather than responses to a change in breathing hole availability.

Even with an apparently homogenous sample of seals, there was significant individual variability in foraging success, behavior, diet, and foraging tactics. Dive depth, duration, distance, and energetic cost were important for explaining foraging success when seals dove in shallow areas where Antarctic silverfish (*Pleuragramma antarcticum*) were more difficult to reach and less abundant. However, the relationship between those variables was not the same for all individuals. Diet and foraging tactics also varied significantly among individuals diving near the coastline. Two coastal seals specialized on silverfish, while two others consumed silverfish and benthic prey. Although benthic prey were more accessible along the coastline than offshore, silverfish, which have a high lipid content, required less handling to consume. Thus, it may be energy-efficient for seals to specialize on silverfish at coastal locations despite the additional time and energy required to travel to depths where silverfish are located. These results helped us understand variability within Weddell seal populations and the basis upon which foraging decisions are made in response to changes in bathymetry, access to breathing holes, and prey abundance and availability.

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Chapter 1: Introduction

Knowledge of the behavior and ecology of diving marine predators has increased markedly over the past 30 years due to new developments in bio-logging technology (i.e., the use of animal-borne instruments to record behavior). Time-depth recorders and satellite-relayed data-loggers have provided information on the depth, duration, and location of dives for species that would have been otherwise impossible to track and observe underwater (e.g., Kooyman, 2004; Block, 2005). Data from these instruments have traditionally been used to construct time-depth profiles which plot depth as a function of dive duration. The shape of time-depth profiles was then used to classify dives (e.g., V-shaped, round bottom, flat bottom) and ecological functions were assigned (e.g., foraging, exploratory, transiting) to groups of dives based on these shapes (e.g., LeBoeuf et al., 1992; Schreer and Testa, 1996; Crocker et al., 1997). A particular emphasis was placed on identifying foraging dives because of the potential benefits that correct conclusions could have on the understanding of predator-prey interactions, food-web dynamics, and optimal foraging strategies (Stephens and Krebs, 1986).

The desire to understand the hunting behaviors of marine predators was so strong that it led to the division of time-depth profiles for foraging dives into periods of descent, ascent, and bottom swimming (i.e., time between descent and ascent) which could be used in the development of optimal foraging models (Simpkins et al., 2001a). Periods of descent and ascent were assumed to represent time spent traveling to and from a patch of prey, while the bottom phase was assumed to represent time spent searching within a patch (e.g., LeBoeuf et al., 1988; Kramer, 1988). These assumptions were based on the idea that foraging depth is an important determinant of foraging success and that air-breathing, diving predators are limited in the time available for foraging within a patch by

the need to replenish their oxygen stores at the surface (Mori, 1998; Thompson and Fedak, 2001). Numerous models were constructed based on these assumptions and were used to predict the optimal balance between the time spent foraging at depth, the time spent in transit to the proper foraging depth, and the time spent at the surface between dives (e.g., Kramer, 1988; Houston and Carbone, 1992; Mori, 1999).

Many conclusions regarding foraging behavior have been based on these models, but the underlying time-depth profiles have important limitations. There is a strong temptation to view time-depth profiles as representing two spatial dimensions, when in fact, they only represent one spatial dimension (depth) and one temporal dimension (Fuiman et al., 2007). Time-depth profiles do not record information about the horizontal movements of an animal and therefore overlook the potentially important ecological movements that take place in this plane (Simpkins et al., 2001a; Fuiman et al., 2007; Wilson et al., 2007). In order to better understand the movements and foraging behaviors of diving marine predators, researchers have developed methods which allow animals to be tracked in three spatial dimensions. Acoustic tracking (Wartzok et al., 1992; Harcourt et al., 2000; Simpkins 2001a-c; Hindell et al., 2002), dead reckoning (Davis et al., 1999, 2003; Wilson et al., 1991, 2007; Fuiman et al., 2007), geomagnetic and acceleration recorders (Mitani et al., 2003, 2004), and digital acoustic recording tags (Johnson and Tyack, 2003) have allowed researchers to go beyond simply recording the duration and depth of diving animals to recording three-dimensional movements and the animal's orientation.

Classification of three-dimensional dives (Harcourt et al., 2000; Simpkins et al., 2001c; Davis et al., 2003) and fine-scale examinations of three-dimensional movements within foraging dives (Simpkins et al., 2001a-b; Fuiman et al., 2007; Wilson et al., 2007) have shown several previous conclusions about foraging behavior to be false. For

example, Harcourt et al. (2000) used an existing classification scheme based on time-depth profiles to classify three-dimensional dive profiles and found that the shape of the three-dimensional dives varied substantially within each dive class. They concluded that important additional information is obtained when three-dimensional data are recorded and should be considered when drawing conclusions about the function of dives. Simpkins et al. (2001a) found that movement in the horizontal plane was the most useful variable for distinguishing movements within the dives of ringed seals (*Phoca hispida*). They used the bimodal frequency distribution of a variable termed "horizontal directionality" to recognize two types of movement: directional and convoluted. They cautiously suggested that directional movement represented travel between patches, while convoluted movements represented travel within a patch. The seals exhibited convoluted movements throughout an entire dive which they believed to be evidence of feeding throughout the duration of a dive. However, Simpkins et al. (2001a) were unable to determine with certainty that convoluted movements were indicative of foraging within a patch since they could not confirm foraging.

The inability to confirm underwater prey encounters has forced many researchers to draw conclusions about foraging behavior based solely on inferences from depth, duration, and occasionally speed data (Davis et al., 1999). Analysis of scats (e.g., Burns et al., 1998; Bowen et al., 2000), regurgitations (e.g., Green and Burton, 1987; Field et al. 2007), stable isotopes (e.g., Burns et al., 1998; Cherel and Hobson, 2007), and fatty acids (Lea et al., 2002; Iverson et al., 2004) were used to determine diet, but none of these techniques allowed for fine-scale examination of feeding over short time periods, such as individual dives or sets of dives (Tinker et al. 2007). To overcome this limitation, researchers developed methods that allow feeding activity to be recorded using jaw movements (Plötz et al., 2001; Liebsch et al., 2007), stomach temperature (Andrews,

1998; Lesage et al., 1999; Baechler et al., 2002; Austin et al., 2006; Khun and Costa, 2006), and vocalizations related to prey capture (Johnson et al., 2004; Miller et al., 2004; Madsen et al., 2005). Other researchers have incorporated still cameras (Hooker et al., 2002; Watanabe et al., 2003) and video cameras (e.g., Marshall, 1998; Davis et al., 1999; Ponganis et al., 2000) into their animal-borne equipment to directly record feeding events. This presents one of the most promising methods for determining the diet and foraging activity of diving marine predators on short time scales.

The ability to simultaneously record information on foraging success and behavior has provided researchers with new insights and conclusions (e.g., Lesage et al., 1999; Mitani et al., 2004; Fuiman et al., 2007). For example, Austin et al. (2006) incorporated time-depth recorders with stomach temperature loggers and found that the most important predictor of foraging success was time spent at the bottom of a dive (i.e., between descent and ascent). However, feeding varied across temporal scales and environmental variation was important at some scales but not at others. Tinker et al. (2007) also examined foraging behavior and diet on a dive-to-dive basis and found individual variability in dietary specialization of sea otters that was reflected in time-depth profiles. Techniques that combine information on foraging behavior and success have provided new insights and resulted in new areas of research, such as individual variability (Tinker et al. 2007).

Currently, the most sophisticated approach available for studying the foraging behavior of diving marine predators involves the simultaneous recording of three-dimensional movements and prey encounters. To date, this information has only been recorded for one pinniped species, the Weddell seal (*Leptonychotes weddellii*; Davis et al., 1999, 2003; Mitani et al., 2003, 2004; Fuiman et al., 2007). There are several advantages to working with Weddell seals: (1) they are large animals that can easily

carry equipment, (2) they are minimally influenced by the presence of humans and can be captured and monitored with relative ease, (3) they are abundant in parts of their range, and (4) their diving behavior and physiology have been well studied using time-depth recorders and satellite-linked time-depth recorders (e.g., Kooyman, 1981; Castellini et al., 1992a-b; Testa, 1994), acoustic tracking (Harcourt et al., 2000; Hindell et al., 2002), dead reckoners (Davis et al., 1999, 2003; Fuiman et al. 2007), and geomagnetic and acceleration recorders (Mitani et al., 2003, 2004). These large predators are highly adapted for hunting in the cold, dark, ice-covered waters of Antarctica, and their hole-breathing behavior and superior diving abilities allow them to live under continuous sea-ice and reach extreme depths (e.g., Kooyman, 1981; Castellini et al., 1992b). They are the only air-breathing predator in Antarctica that is capable of foraging in both the pelagic and benthic habitats of the ice-covered waters of the Antarctic continental shelf (Lake et al., 2003). The diet of Weddell seals in McMurdo Sound primarily consists of small notothenoid fishes such as Antarctic silverfish (*Pleuragramma antarcticum*) and *Trematomus* spp. However, they do occasionally feed on other prey items such as Antarctic toothfish (*Dissostichus mawsoni*), bald notothen (*Pagothenia borkgrevinki*), icefishes, mysids, decapod and amphipod crustaceans, octopus, and squid (e.g., Castellini et al., 1992b; Burns et al., 1998; Davis et al., 1999).

Of those studies which have simultaneously recorded three-dimensional movements and foraging events in Weddell seals, one has identified foraging dives and described their overall characteristics. Davis et al. (2003) used a multivariate classification method to identify four distinct types of diving behavior. The presence of prey on the video record revealed that foraging occurred during Type 1 dives, which were intermediate in duration, deep, and had steep descent and ascent angles. Type 1 dives were similar to the presumed foraging dives from two previous classifications based on

time-depth profiles (Kooyman, 1968; Schreer and Testa, 1996), but Type 1 dives had a wider range of depth and duration than the foraging dives of Kooyman (1968), and the criteria for foraging dives established by Schreer and Testa (1996) misclassified several Type 1 dives as non-foraging dives. However, the isolated-hole protocol used by Davis et al. (2003) restricted the seals to a single breathing hole and prevented them from interacting with other seals. It is possible that the isolated-hole protocol could limit the variety of behaviors used by the seals for foraging and a future classification of free-ranging diving behavior could provide new information about the foraging behavior of Weddell seals.

Two studies (Mitani et al., 2004; Fuiman et al., 2007) have examined the fine-scale structure within Weddell seal foraging dives using three-dimensional movements and foraging success. Mitani et al. (2004) subdivided three-dimensional foraging dives into periods of descent, ascent, and bottom swimming, and found that the descent and ascent phases were more linear than the bottom phase. The convoluted movements of the bottom phase were also associated with a higher number of prey encounters (estimated from still video images; Watanabe et al., 2003). They concluded that the bottom phase of a dive represented the time spent foraging within a prey patch, while the descent and ascent phases represented the time spent traveling to and from a patch (Mitani et al., 2004). This supported previous assumptions based on time-depth profiles in which the bottom phase of a dive was assumed to represent the amount of time spent foraging in a patch (e.g., LeBoeuf et al., 1988; Kramer, 1988).

Fuiman et al. (2007) also examined the behavior within three-dimensional foraging dives of Weddell seals, but at a finer resolution. They identified nine behavioral states and five prey-related events based on the geometry of the three-dimensional dive path, changes in speed and stroking, and video imagery. Encounters with Antarctic

silverfish were the most common prey-related event and were most frequently preceded by ascent, but descent and horizontal swimming also led to encounters with these small, midwater fishes. These results confirmed that discontinuous trajectories in some time-depth profiles, which were the result of switching between descent, ascent, and horizontal swimming, were an indication of encounters with midwater prey. Fuiman et al. (2007) also examined the dominant sequence of behaviors leading to the first silverfish encounter in a dive in order to better understand the hunting tactics used by Weddell seals to locate small, midwater prey. The first silverfish encounter was most commonly preceded by ascent, and this period of ascent was preceded by horizontal swimming, which was in turn preceded by descent and meandering descent. They interpreted this sequence as the seals searching for prey during the descent phases of a dive, pursuing prey horizontally while the prey flee upward, and finally ascending to attack prey. Reduced stroking rates and increased amounts of gliding (i.e., lack of stroking of the hind flippers) observed during the descent phases of a dive suggested that descent and meandering descent were used for searching. Fuiman et al. (2007) inferred that when seals are gliding, the amount of self-generated noise is reduced, allowing seals to be more attentive to signals from prey. The alternating right and left hand turns characteristic of meandering descent were also an indication that seals were searching during this state. The lateral excursions were thought to expand the seal's search path, enhancing the likelihood of perceiving signals from prey (Fuiman et al., 2007). However, this study was also based on data from an isolated-hole, and therefore, might not represent entirely natural behavior.

The studies comprising this dissertation are based on data collected from adult Weddell seals in McMurdo Sound, Antarctica, equipped with video data recorders (VDRs). Unlike previous studies, however, the seals were not restricted to a single

breathing hole and were free to travel throughout the study area and interact with other seals. The primary objective of these studies is to gain a more complete idea of the natural foraging behavior of Weddell seals. Specific goals were to: (1) identify the foraging dives of free-ranging Weddell seals using video confirmation (Chapter 2), (2) compare individual seals for differences in foraging success and behavior (Chapter 3), (3) compare results of free-ranging seals with seals diving at an isolated-hole (Chapter 4), and (4) determine the degree of individual variability in diet and foraging tactics of free-ranging Weddell seals (Chapter 5).

Video and data were collected for 234 dives from eight seals during the 2001 and 2002 field seasons. All 234 dives were included in Chapter 2 and used to identify foraging dives of free-ranging Weddell seals. Only those dives identified as foraging for the 2002 field season were included in the analyses for Chapters 3-5. Dives from the 2001 field season were eliminated since a small number of foraging dives were identified for each individual. In Chapter 3, the six seals foraging along the coastline of Tent Island were compared for differences in foraging success and behavior. Separate comparisons of success and behavior were also made between the two seals diving offshore. In Chapter 4, three-dimensional foraging dive paths of two free-ranging offshore seals were compared with three-dimensional foraging dive paths of six seals foraging at an isolated breathing-hole in 1998 and 1999. Isolated-hole data from Fuiman et al., 2007 was used for this comparison. In Chapter 5, individuals diving at Tent Island were compared for differences in diet and foraging tactics. A separate comparison of offshore seals was also conducted.

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Chapter 2: Identification of foraging dives in free-ranging Weddell seals (*Leptonychotes weddellii*): Confirmation using video records

ABSTRACT

Understanding foraging behavior is important for addressing ecological questions for all predators, but is particularly challenging for air-breathing marine vertebrates. The inability to directly observe this group underwater has made it difficult to classify and understand foraging behaviors with certainty and accuracy. To determine the underwater behavior of one air-breathing marine predator, free-ranging, adult Weddell seals were equipped with animal-borne video and data recorders (VDRs). Eighteen dive descriptors summarizing the duration, depth, speed, stroking frequency, gliding, and energetic cost of 234 dives were calculated. Dive descriptors were included in non-hierarchical cluster analyses that identified five distinct groups of dives. Eight of the 18 dive descriptors contributed strongly to the discrimination between groups. Presence of prey on the video record confirmed Groups 1, 4, and 5 as foraging dives. Group 1 dives were deep and exceeded the estimated aerobic dive limit, while Group 4 dives were also deep but probably remained aerobic. Group 5 dives were shallow and aerobic. Comparisons with prior classifications showed that deep aerobic dives were similar to foraging dives identified previously, but shallow aerobic and deep anaerobic dives represented new foraging categories. The proportion of successful dives and the number of prey encountered per successful dive varied among groups and locations. The distribution of foraging dive types also varied among these locations, and appeared to result from the depth of silverfish, the main prey item in this region, and bathymetric variability. Seals diving along the coast used more deep anaerobic and shallow aerobic dives, while deep aerobic dives were most common offshore. This suite of foraging dive types shows how

Weddell seals deal with trade-offs between the energetic cost of traveling to prey, the likelihood of encountering prey at certain depths, and the need to remain along coastlines to breed.

INTRODUCTION

The diving behavior of air-breathing marine vertebrates consists of a series of movements and events that can be divided into discrete units for behavioral analysis. In most cases, a repertoire of stereotyped movements exists that can be easily distinguished (i.e. modal action patterns), although some variability exists within these characteristic behaviors (Hinde, 1982). The types of behavioral categories defined, particularly the extent to which they are specific rather than general, depends on the scope of the question being asked (Martin and Bateson, 1993). Examples of several broad, general categories include: reproduction, foraging, communication, and traveling. When the question is more specific, it becomes necessary to divide these general behavioral acts into their component parts (Martin and Bateson, 1993; Lehner, 1996). For example, foraging behavior can be subdivided into search, pursuit, and handling. The capacity to identify behavioral categories, whether specific or general, usually relies on a researcher's ability to observe the animal (Hinde, 1982).

For many years, the challenges associated with monitoring the underwater excursions of free-ranging diving mammals have made it difficult to classify their behavior with certainty (Davis et al., 2003; Fuiman et al., 2007). Methods such as SCUBA, fixed-location cameras, remotely operated vehicles, and manned submersibles provide only short glimpses of highly mobile animals (Davis et al., 1999; Kooyman, 2004; Block, 2005). New developments in bio-logging technology (i.e., the use of animal-borne instruments to gather data) have helped overcome some of these challenges. The use of time-depth recorders and satellite-linked time-depth recorders to collect information about the depth, duration, and location of dives has greatly increased the knowledge of diving behavior and movements of large marine vertebrates (e.g., Fedak et

al., 2002; Kooyman, 2004; Block, 2005). More recent developments in acoustic tracking (e.g., Wartzok et al., 1992; Harcourt et al., 2000; Simpkins, 2001), dead reckoning (Wilson et al., 1991; Davis et al., 1999), geomagnetic and acceleration recorders (Mitani et al., 2003, 2004), and digital acoustic recording tags (Johnson and Tyack, 2003) have allowed researchers to surpass recording just time and depth of diving animals to recording three-dimensional movements and body orientation of submerged predators.

These techniques have provided many new insights into the behavior and ecology of diving animals, but none enable direct observation of behavior at depth. Researchers have frequently used time, depth, and swimming speed data to classify dives and to assign ecological functions such as foraging, exploration, and transiting (e.g. Hindell et al., 1991; LeBoeuf et al., 1992; Crocker et al., 1997). Identification of foraging dives is particularly important because of the potential benefits that correct conclusions could have on the understanding of predator-prey interactions, energetic efficiency, and optimal foraging strategies (Stephens and Krebs, 1986). Some researchers have added additional sensors that record stomach temperature, jaw movements, and vocalizations, in attempts to confirm prey encounters (e.g., Lesage et al., 1999; Plötz et al., 2001; Johnson et al., 2004), while other researchers have used animal-borne still cameras and video cameras to directly confirm underwater feeding events (e.g., Marshall, 1998; Davis et al., 1999; Hooker et al., 2002; Watanabe et al., 2003). These methods have already shown that some of the previous inferences about foraging behavior were incorrect (Lesage et al., 1999; Davis et al., 2003).

The diving habits of Weddell seals (*Leptonychotes weddellii*) have been well studied using time-depth recorders and satellite-linked time-depth recorders (e.g., Kooyman, 1981; Castellini et al., 1992; Testa, 1994), acoustic tracking (Harcourt et al., 2000; Hindell et al., 2002), dead reckoning (Davis et al., 1999, 2003), and geomagnetic

and acceleration recorders (Mitani et al., 2003, 2004). These seals are highly adapted for hunting in the cold, dark, ice-covered waters of Antarctica (Kooyman, 1981; Castellini et al., 1992). Their hole-breathing strategy and ability to dive to extreme depths allows them to hunt in both the pelagic and benthic environments of the Antarctic continental shelf (Lake et al., 2003). The diet of Weddell seals in McMurdo Sound has been shown to vary little and consists primarily of small nototheniid fishes such as silverfish (*Pleuragramma antarcticum*) and *Trematomus* spp. (e.g., Castellini et al., 1992; Burns et al., 1998; Davis et al., 1999). However, other types of prey are available, and the seals are known to feed occasionally on Antarctic toothfish (*Dissostichus mawsoni*), *Gymnodraco* spp., icefishes, mysids, decapod and amphipod crustaceans, octopus, and squid (e.g., Dearborn, 1965; Testa et al., 1985; Davis et al., 1999).

Two previous studies have classified the diving behavior of free-ranging Weddell seals using data collected with time-depth recorders. Kooyman (1968) used a manual approach to categorize diving behavior and found three distinct dive types. Of these, Pattern III dives were assumed to involve foraging since they were numerous, reached 300-400 m, lasted 8-14 min, and contained steep rates of ascent and descent. Schreer and Testa (1996) used a multivariate classification method to identify six distinct dive types. Two of these were believed to be foraging dives. The first group was termed midwater foraging dives that were characterized by deep time-depth profiles with multiple small ascents and descents along the bottom of the dive. The second group also had deep time-depth profiles but without multiple, small ascents and descents along the bottom part of the dive. These were assumed to be benthic foraging dives. More recently, Davis et al. (2003) classified Weddell seal diving behavior at an isolated hole using an animal-borne video and data recorder (VDR) that enabled the calculation (dead reckoning) of three-dimensional movements. This was the first classification of marine mammal diving

behavior to use video observations of prey encounters to confirm foraging events at an isolated hole. Four types of dives were identified using a multivariate classification method, and the presence of prey on the video record revealed that foraging occurred during Type 1 dives. Type 1 dives were similar to the presumed foraging dives from two previous classifications based on time-depth profiles (Kooyman, 1968; Schreer and Testa, 1996), but Type 1 dives had a wider range of depth and duration than the foraging dives of Kooyman (1968), and the criteria for foraging dives established by Schreer and Testa (1996) misclassified several Type 1 dives as non-foraging dives. However, the isolated-hole protocol used by Davis et al. (2003) restricted the seals to a single breathing hole and prevented them from interacting with other seals or ranging beyond a 4-mile radius. It is possible that the isolated-hole protocol limits the variety of behaviors used by the seals for foraging and a classification of free-ranging diving behavior could provide new information about the foraging behavior of Weddell seals.

In the current study, 13 adult Weddell seals were equipped with the same VDRs used by Davis et al. (2003), but unlike the isolated-hole study, these seals were free-ranging (i.e., not restricted to a single breathing hole and free to move throughout the study area). This allowed for (1) comparison of current classification results with results from previous studies and (2) investigation of how foraging behavior varied at different locations within the study area. Results indicate that there were five distinct diving patterns in free-ranging Weddell seals, three of which were recognized as foraging dives by the presence of prey on the video record.

METHODS

Animal capture and instrumentation

Thirteen adult Weddell seals were captured near Ross Island, McMurdo Sound, Antarctica (Figure 1) from October to November of 2001 and 2002, of which eight seals (7 females, 1 male; body mass = 432.6 ± 75.6 Kg [mean ± SD]; standard length = 239.9 ± 9.0 cm) were included in the current analysis due to instrument failure and data errors in some deployments (Table 1). Capture and instrumentation methods have been described by Davis et al. (1999). Briefly, seals were captured on the sea ice using a purse-string net and were transported to a field camp using a specially designed sled. Upon arrival at the field camp, animals were sedated (ketamine and diazepam), weighed, and measured. After cleaning the fur with acetone, a piece of thin neoprene rubber (ca. 30 cm in diameter) was glued to the seal's back using contact cement. The neoprene rubber provided a secure but flexible attachment for the main housing of the VDR. The main housing (35 cm long x 13 cm in diameter) was placed in a molded, non-compressible foam cradle and secured to the neoprene rubber with a hose clamp, Velcro and plastic cable ties. The foam cradle offset the weight of the instruments so the unit was neutrally buoyant in water. The video camera (6 cm long x 6 cm in diameter; mounted on the head), compass housing (17 cm long x 5.5 cm in diameter; placed behind the main housing) and accelerometer (6 x 3 x 2 cm; located near the base of the tail) were glued to the fur using the same method. A satellite transmitter and two VHF radio transmitters were also glued to the fur to enable use to relocate the seals once they were released. Each animal was allowed to recover from anesthesia for about 18 h before it was released into a 1.3-meter diameter man-made breathing hole at the field camp.

The instruments were typically deployed for 3-5 days before the seals were relocated and had their instruments changed for additional deployments (1-6 deployments

per seal). When the seals hauled out on the ice, the satellite transmitters provided the seal's location to within one-half km radius, and VHF radio transmitters enabled the seal's exact location to be determined using a receiver and directional antenna. All animal-handling procedures were in accordance with animal use protocols of The University of Texas at Austin and Texas A&M University.

Equipment

The self-contained video camera and data logger were designed to record the behavior, swimming performance, three-dimensional movements, and environment immediately in front of diving animals, and have previously been described by Davis et al. (1999). To summarize, the data logger was contained in a torpedo-shaped, aluminum housing. The data logger was designed to record data from several instruments: (1) a low-light sensitive, monochrome video camera, surrounded by an array of near-infrared light-emitting diodes and located on the animal's head, (2) a pressure transducer, (3) a water speed sensor (paddle wheel), (4) a gimbaled flux-gate compass, and (5) a small 1-axis accelerometer placed on the dorsal surface near the base of the seal's tail to record flipper stroking. Pressure, speed, and bearing were sampled once per second, the accelerometer was sampled 16 times per second, and the camera recorded at a rate of 30 frames per second. The diodes enabled the camera to record images underwater in complete darkness up to a distance of ca. 1 m and further when additional ambient light was available. The infrared light source (λ_{max} = 850 nm) was assumed to be invisible to the seals and their prey (Lavigne et al., 1977), which did not interfere with normal behavior of the seals or their prey. The pressure transducer was calibrated in the laboratory for water depth. The compass was calibrated at the deployment site using the position of the sun together with GPS location, time, and a navigation computer. The speed sensor was calibrated after each deployment using the method of Blackwell et al.

(1999). Although it is difficult to determine with certainty the effect of the equipment on the behavior of the animal, the additional hydrodynamic drag created by the VDR did not result in significant differences in the recovery oxygen consumption for seals diving with and without the equipment (Williams et al., 2004). The frontal area of the video camera and data logger occupied < 5.5% of the frontal area of the seal. Also, the seals continued to feed successfully while carrying the equipment, which suggests that the instrumentation did not have a detrimental effect on foraging behavior.

The location of dives was determined by gathering the GPS locations of several breathing holes within the study area using handheld GPS units and placing distinct markers in each hole so they could be identified on the video record and matched to the handheld GPS coordinates. When the seals failed to surface in a marked hole, observations of distinctive underwater features (e.g., continental slope of Tent Island, the Erebus Ice Tongue) on the video record were used to place the seals within a general geographic context.

Data analysis

Identification of dive groups

Data and video were downloaded immediately upon recovery of the instruments. Each video tape was duplicated in VHS format and a time code was superimposed on the video display to facilitate later analysis. The video tapes were reviewed for scenes of interest (e.g. encounters with prey, visible substrate, hole markers) and used to build a database of prey encounters. Interactions with several different types of prey were documented on the video record (Figure 2). These included encounters with silverfish (*Pleuragramma antarcticum*), *Trematomus* spp., bald notothen (*Pagothenia borchgrevinki*), icefish, squid, octopus, krill, and several unidentifiable prey items. The

type, number, and time of each prey encountered (i.e., prey located less than 1 m from the seals muzzle but ingestion of prey not always evident) was recorded for each dive. Video and data were gathered for 234 dives (6-60 dives per seal). Eighteen variables (Table 2) were computed to describe each dive based on characteristics of time, distance, speed, stroking of the hind flippers, gliding (defined as 3 continuous seconds with no stroking of the flippers), and energetic cost. Energetic cost was calculated for each dive from the equation provided by Williams et al. (2004) for non-feeding Weddell seals. This equation estimates oxygen consumption during a dive from the seal's body mass, duration of the dive, and the number of strokes of the hind flippers. It does not take into account the added cost associated with processing a meal (i.e., heat increment of feeding), but was chosen because it provided a standard method for calculating energy consumption throughout the entire course of a dive. Energy flux (mL O_2 kg^{-1} min^{-1}) was calculated by dividing the total energetic cost (mL O_2 kg^{-1}) of a dive by dive duration.

Failures of the GPS unit to register a position while the seal was at the surface allowed only 114 dives to be reconstructed in three-dimensions. Therefore, in order to maintain a larger sample size, no variables describing the three-dimensional structure of a dive were included in the analysis. Davis et al. (2003) found that foraging dives of Weddell seals diving from an offshore, isolated hole could be easily distinguished without using three-dimensional variables. In that study, foraging dives were correctly identified 92% of the time using dive duration, depth, and speed statistics (Davis et al., 2003).

Dives were grouped based on similarities in duration, depth, speed, stroking of the hind flippers, gliding, and energetic cost using a *k*-means cluster analysis. This non-hierarchical clustering method was chosen because it does not impose relationships upon the groups. All variables were standardized to a mean of 0 and a SD of 1 before applying

the clustering procedure. Since *k*-means clustering requires the number of groups be defined *a priori* and the appropriate number of groups was unknown, seven cluster analyses were performed specifying a different number of groups in each, ranging from two to eight groups. Groups that contained less than 7% of the total dives (N = 16) were considered outliers, or rare types of diving behavior, and were disregarded. Results of the cluster analysis were then combined with the jackknifed cross-validation percentages of a subsequent discriminant analysis to determine the final number of dive groups. Discriminant analysis was also used to determine whether the groups were significantly different (Wilks' Lambda value) from one another and which variables, or combinations of variables, contributed strongly to the separation. A variable was considered important in the discrimination if the absolute value of the standardized canonical coefficient was high relative to the other variables. The discriminant analysis was conducted using raw values and a forward stepwise procedure with a tolerance level of 0.001 to add variables to the analysis. All statistical analyses were performed with Systat statistical software (version 10.2; Systat Software Inc.).

Geographic variability

Diving occurred in three distinct geographic regions within McMurdo Sound (Figure 1) and contingency table analyses were used to determine whether diving behavior varied among these regions. Seals 19 and 20 dove south of the Erebus Ice Tongue along a perennial tidal crack extending south of the Erebus Ice Tongue. Seals 25 – 31 used breathing holes located along the western coast of Tent Island. Seals 25 and 26 traveled away from Ross Island and dove at several offshore breathing holes located over the deeper waters of McMurdo Sound. A two-way contingency table was used to test for independence of the distribution of foraging dive groups among the three regions (Pearson's chi-square). Expected values for each region (Table 6) met the requirements

of contingency table analysis (all cells with expected frequencies > 5) and all regions could therefore be included in the analysis (Lehner, 1996). Standardized deviates were used to characterize departures of the observed values from expected values for each analysis.

RESULTS

Identification of dive groups

Seven separate cluster analyses were used to classify the 234 dives. When two to five groups were defined, the number of dives allocated to each cluster exceeded 29. When six to eight groups were specified, there was at least one group present with fewer than 16 dives (less than 7% of the total number of dives). This suggested that a maximum of five groups could be defined before the cluster analysis created artificial groupings. This was supported by the jackknife cross-validation values of the subsequent discriminant analysis. Overall jackknife classification values ranged from 90 to 97%. When five groups were specified the jackknife classification success was 94%, indicating the presence of uniquely defined groups. The only classification procedure with a higher value was two groups (97%). However, group size data does not support the presence of two groups since additional groups could be defined without group size decreasing below 7% of the total number of dives. When six, seven, or eight groups were specified, jackknife classification values were 93, 90, and 90%, respectively.

The discriminant analysis also showed that the five groups were significantly different from one another (Wilks' Lambda = 0.002, $p < 0.001$). All 18 dive descriptors were included in the analysis. Jackknife classification success was high, with only a small number of misclassifications (14) for the five dive groups (Table 3). The presence of prey, as recorded on the video tape, was used to determine which of the five dive

groups were used for foraging. Groups 1, 3, 4, and 5 contained at least one dive with a prey encounter (Table 3). Groups 1, 4, and 5 were assumed to be foraging dives because of the high percentage of prey encounters in each of these groups (75.0, 82.4, and 20.7% respectively). Groups 2 and 3 were assumed to be non-foraging dives because of the very low occurrence of prey encounters (0.0 and 2.4% respectively [Table 3]). Dives in Groups 1, 4, and 5 in which the seal did not encounter prey were considered to be unsuccessful foraging dives.

The three groups of foraging dives (1, 4, and 5) were separated from the two non-foraging groups (2 and 3) primarily by discriminant axis 1 (DA1 [Figure 3a]). DA1 had the highest discriminatory power with an eigenvalue of 12.7. Eight variables had high loadings on DA1 and were responsible for the separation along this axis (Figure 3b, Table 4). Many of the same variables were also responsible for the small amount of separation contributed by DA2 (eigenvalue of 4.1 [Figure 3, Table 4]). Dive descriptors characterizing the depth, duration, stroking of the hind flippers, and energetic cost of a dive were important in the separation along DA1 and DA2, but none of the descriptors for speed or gliding contributed to the separation. DA3 and DA4 contributed very little to the overall discrimination of dive groups (eigenvalues of 2.3 and 1.6 respectively).

Description of dive groups

Groups 1, 4, and 5 each represented a distinct type of foraging dive (Figure 4). Mean values for seven of the eight important dive descriptors (as determined by the discriminant analysis) were greatest for Group 1 dives (Table 5; Figure 5). During these dives, seals reached the greatest mean and maximum depths and spent the most time at depths where silverfish were expected to be present (deeper than 155 m – the mean minimum depth of all silverfish encounters in the current study). They also had the longest total dive duration and contained the greatest number of total strokes. The long

duration and increased number of strokes during Group 1 dives resulted in the highest energetic cost of any foraging group (Figure 5). Based on the estimated total available body oxygen stores of an average adult Weddell seal (67 ml O_2 Kg^{-1} [Kooyman, 1989]), the energetic cost of Group 1 dives generally exceeded available oxygen stores (Table 5) and is an indication that the seals may have relied on anaerobic metabolism. Average flipper stroke rate was the only discriminating variable that was not the highest for Group 1 dives. Successful Group 1 dives had a similar number of prey encounters as Group 5 dives, but contained fewer prey encounters than Group 4 dives (Table 5, Figure 5).

In Group 4 dives, average values for six of the eight important dive descriptors were intermediate between Groups 1 and 5 (Table 5; Figure 5). These dives were relatively deep, but shallower (by 8.0%) than Group 1 dives. Time spent at depths where silverfish were expected was also slightly less than in Group 1 dives. However, these dives were deeper than Group 5 dives (by 48.0%). Although they were similar in duration to Group 5 dives, Group 4 dives were the shortest of the three foraging dive types. They had the highest stroking rate, which resulted in a noticeably higher number of total strokes than Group 5 dives. However, they still exhibited fewer total strokes than Group 1 dives. The shorter duration and decreased number of strokes during Group 4 dives, compared to Group 1, resulted in a lower total energetic cost. The average estimated energetic cost of Group 4 dives was within the available oxygen limits of Weddell seals (Table 5), which suggests they were not relying on anaerobic metabolism. Successful Group 4 dives contained the highest number of prey encounters of any foraging group (Table 5, Figure 5).

Average values for seven of the eight important dive descriptors were lowest for Group 5 foraging dives (Table 5; Figure 5). They were the shallowest of all foraging dive types, and the seals spent the least amount of time below depths where silverfish

were expected. Group 5 dives were only slightly longer in duration than Group 4, but were much shorter than Group 1 dives. Despite the similarities in duration between Groups 4 and 5, Group 5 dives showed a noticeably lower flipper stroke rate, which resulted in the lowest number of total strokes for any foraging group. This also resulted in a much lower energetic cost than Group 4 dives, which means seals expended the least amount of energy when foraging during Group 5 dives (Table 5). Successful Group 5 dives contained a similar number of prey encounters as Group 1 dives, but there was greater variability (Table 5, Figure 5). The three foraging dive types were given descriptive names based on their depth and energetic cost; Group 1 dives were deep anaerobic foraging behavior, Group 4 dives were deep aerobic foraging behavior, and Group 5 dives were shallow aerobic behavior.

Geographic variability

Weddell seals foraged at three different geographic locations within McMurdo Sound (Figure 1), and this had a significant effect (Pearson chi-square = 70.0, $P < 0.001$) on the frequency of the three foraging dive groups (Table 6, Figure 6). Standardized deviates showed that seals performed significantly more deep anaerobic (Group 1; n = 37) and shallow aerobic dives (Group 5; n = 25) along the west coast of Tent Island, while performing significantly fewer deep aerobic dives (Group 4; n = 12). The opposite was true for the two seals diving offshore in the deeper waters of McMurdo Sound. In this location, seals used significantly more deep aerobic dives (Group 4; n = 53) and significantly fewer deep anaerobic (Group 1; n = 5) and shallow aerobic dives (Group 5; n = 3). Observed values were not significantly different from expected values for the seals diving south of the Erebus Ice Tongue, but it is worth noting that deep aerobic dives (Group 4; n = 9) were more abundant than deep anaerobic (Group 1; n = 2) and shallow

aerobic dives (Group 5; $n = 1$). This was similar to the pattern observed at the offshore breathing holes (Table 6).

The geographic variability in dive groups resulted from a combination of the depth at which silverfish were encountered and bathymetric differences among the three locations. South of the Erebus Ice Tongue and at the offshore region, breathing holes were located over deeper water and away from shallow coastal waters. This made it easier for the seals to forage at depths where silverfish commonly occur. Along the west coast of Tent Island, the seals were forced by the shallow bathymetry to descend at a much slower rate and to travel farther offshore (i.e., horizontal movement) to reach depths where silverfish occur. To test this hypothesis, the three locations were compared for differences in the depth and elapsed time to the first silverfish encounter. Silverfish were expected to be found at the same depth in all three locations, but were predicted to be encountered significantly later along the coastline of Tent Island since the seals had to travel farther horizontally to reach the same depths. No significant differences were found among the three locations in the depth of the first silverfish encounter (ANOVA; $F_{2,91} = 2.2$, $P = 0.114$), but there were significant differences in the time of the first encounter (ANOVA; $F_{2,91} = 50.7$, $P < 0.001$). Post hoc comparisons using Bonferroni corrections showed that the seals encountered the first silverfish in a dive significantly ($P < 0.05$) later along the coast of Tent Island (10.6 ± 0.5 min [mean ± SE]) than they did near the Erebus Ice Tongue (6.5 ± 0.9 min) or at the offshore location (5.8 ± 0.2 min).

DISCUSSION

Free-ranging Weddell seals in McMurdo Sound use a range of foraging dives to locate prey. Three distinct foraging groups were identified in the current study, and the frequency at which these groups were used varied with location. The dominant type of foraging dives performed at each location appeared to be determined by the preferred

depth of silverfish, the main prey item of Weddell seals in McMurdo Sound (e.g., Castellini et al., 1992; Burns et al., 1998; Davis et al., 1999), and by bathymetry. Silverfish constituted 98.9% of the seals' diet in the current study, and encounters with silverfish occurred between 192.1 ± 8.0 m (mean minimum depth ± SE) and 318.4 ± 6.4 m (mean maximum depth ± SE).

Seals diving at Tent Island used more deep anaerobic foraging dives (Group 1) than seals diving offshore and south of the Erebus Ice Tongue. The video record showed that 75% of deep anaerobic dives contained at least one prey encounter, and seals averaged close to eight prey encounters per successful dive. The majority of encounters were with silverfish (96.1%), but a small number of benthic prey encounters (3.5%) was also observed. All benthic encounters (n = 6) occurred along the coastline of Tent Island. Seals in this region swam along the continental slope, as evidenced by the presence of the seafloor on the video record, while traveling to the depths where silverfish typically occur. Therefore, the small number of benthic encounters was most likely the result of seals feeding opportunistically as they swam to and from deeper waters.

Following the continental slope at Tent Island forced seals to travel farther horizontally in order to find and forage in patches of silverfish. The first silverfish encounter in a dive occurred significantly later in dives originating along the coast. This resulted in longer dive durations, greater distances traveled, and higher energetic costs characteristic of deep anaerobic dives, and explains the presence of more deep anaerobic dives originating from the coastline. There was only a small number of deep anaerobic dives that occurred over deeper water, and the dives that did occur in these locations may have resulted from the seals' inability to initially locate prey, causing the seals to forage more extensively.

Seals diving at Tent Island also performed a greater number of shallow aerobic foraging dives (Group 5) than seals diving at offshore breathing holes. The video record showed that over 20% of shallow aerobic foraging dives contained at least one prey encounter. Although the percentage of successful dives was less for shallow aerobic dives than it was for deep aerobic and deep anaerobic dives, the success rate of shallow aerobic dives was similar to that of deep anaerobic dives (8 encounters per dive). This suggests that shallow aerobic dives were not just incidental encounters but represent another type of foraging behavior. The average depth of the first silverfish encounter during shallow aerobic dives (142.3 ± 13.9 m) was significantly shallower (ANOVA; $F_{2,91} = 19.5$, $P < 0.001$) than in deep anaerobic (309.1 ± 10.7 m) and deep aerobic (306.3 ± 7.6 m) dives. The shorter durations, lower stroking rates, and shallower depths of prey encounters associated with this type of foraging behavior could indicate an energy-saving foraging strategy in which the seals were exploiting shallow schools of silverfish. If capture rates are similar for deep anaerobic and shallow aerobic dives, the ratio of energy gained to energy expended (i.e., net energy gain) will be much higher for shallow aerobic dives.

Although shallow aerobic foraging dives were performed at a higher frequency at Tent Island, the percentage of successful shallow aerobic dives (10%) was lower at this location than it was at the two offshore locations. The three shallow aerobic dives that occurred at offshore breathing holes all resulted in silverfish encounters. Only one shallow aerobic dive occurred south of the Erebus Ice Tongue and was unsuccessful. When the successful, shallow, aerobic dives at Tent Island were compared with the successful dives at offshore breathing holes, the offshore dives had a greater number of encounters (3.7 ± 2.2 vs. 11.7 ± 3.5 encounters per dive). Thus, shallow aerobic diving appears to be a less successful foraging strategy at Tent Island, but it is an energy

efficient strategy if the seals are able to capture prey. The increased frequency of shallow aerobic dives at Tent Island suggests that seals in this location were attempting to exploit shallow schools of prey more often than the seals foraging offshore. However, the lower success rate of shallow aerobic dives at Tent Island indicates that shallow prey may be less available in this region and could explain the abundance of deep anaerobic dives. In other words, when seals were unable to locate shallow schools of prey along the coast, they had to expend more time and energy traveling to depths where silverfish were typically more abundant. Future analysis of the sequence of dive types could reveal more about the function of this type of foraging behavior.

Seals diving offshore and south of the Erebus Ice Tongue used more deep aerobic foraging dives (Group 4) than seals diving along the coastline. The video record showed that over 82% of deep aerobic dives contained at least one prey encounter and that silverfish constituted 98.9% of the seals' diet during these dives. Deep aerobic dives were the most successful foraging group, averaging over 16 prey encounters per dive. When seals foraged from breathing holes over deep water (ca. 500 m) they were not forced to follow the continental slope and were able to spend less time, travel a shorter distance, and expend less energy to reach the depths where silverfish typically occurred. This explains why the first silverfish encounter in a dive occurred significantly earlier at both offshore locations than it did at Tent Island.

Results from the current study show similarities with prior dive classifications for Weddell seals, but comparisons with these studies also indicated that seals use a wider range of foraging dive types to locate prey than previously thought. Based on time and depth statistics, deep aerobic dives were similar to the foraging dives identified in three previous classification studies (Kooyman, 1968; Schreer and Testa, 1996; Davis et al., 2003). Deep anaerobic dives were also similar in depth and duration to the benthic

foraging dives identified previously by Schreer and Testa (1996), but evidence from the video record suggests that these dives were not indicative of benthic foraging. There were very few benthic encounters observed and seals did not always reach the sea floor during deep anaerobic dives. Instead, Weddell seals appear to use these dives to travel to silverfish depths from breathing holes along the coastline or to forage more extensively offshore when prey are difficult to find. Shallow aerobic dives were similar in depth and duration to the Type 3 dives identified by Schreer and Testa (1996), but in their study a foraging function was not proposed for this group. Rather, Schreer and Testa (1996) hypothesized that the seals were either following the slope of the sea floor as they descended or were exploring the area for future foraging opportunities. The video record showed that the bottom was visible in all but one dive at Tent Island, which might suggest that seals were following the coastal slope in this region. However, the sea floor was never observed during the shallow aerobic dives at the two offshore locations and seals successfully encountered prey at a relatively high frequency during these dives. This indicates that shallow aerobic dives are a type of foraging behavior that had previously not been identified as such.

In summary, three groups of foraging dives were identified for free-ranging Weddell seals. The distribution of foraging groups varied among locations, and the type of dives performed at each location was determined by the depth of silverfish and bathymetric variability within McMurdo Sound. The proportion of successful dives and the average number of encounters per successful dive varied among groups and locations. Seals diving along the coast used more deep anaerobic and shallow aerobic dives. Deep anaerobic dives required more energy than shallow aerobic dives, but the percentage of successful dives was higher for deep anaerobic dives. For seals foraging along the coast, there may be an interesting trade-off between expending less energy to forage at depths

where silverfish are less abundant and expending more energy to forage at depths where the opportunities for encountering silverfish are greater. This trade-off could be especially important since Weddell seals tend to congregate and forage along coastlines during the summer breeding season (Kooyman, 1968; Castellini et al., 1992; Testa, 1994). When seals foraged away from the coast they used more deep aerobic dives. These dives required less time and energy to travel to silverfish depths than deep anaerobic dives and resulted in more silverfish encounters. This suggests that foraging offshore using deep aerobic dives is a very efficient strategy. However, another important trade-off could exist between foraging close to Tent Island where the seals' chances of breeding successfully are higher and expending time and energy to travel offshore where foraging is more efficient.

Identification of a range of foraging behaviors shows how Weddell seals deal with the trade-offs between energetic cost of traveling to prey, likelihood of encountering prey at certain depths, and the need to remain along coastlines to breed. Comparisons with Weddell seals diving in other areas of Antarctica could provide further information about how foraging strategies change according to prey type and bathymetry.

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Table 1. Sample size (dives with both data and video), capture year, sex, mass, and length of 8 free-ranging Weddell seals (*Leptonychotes weddellii*) instrumented from October to November, 2001 and 2002, in McMurdo Sound, Antarctica.

Seal No	N	Year	Sex	Mass (Kg)	Length (cm)
19	28	2001	Female	316.1	240.0
20	6	2001	Male	363.4	227.0
25	60	2002	Female	391.0	231.5
26	58	2002	Female	428.4	246.0
27	32	2002	Female	459.2	232.0
28	13	2002	Female	466.6	245.0
29	28	2002	Female	559.8	253.5
31	9	2002	Female	476.0	244.0

Table 2. Descriptors used to describe dives of free-ranging Weddell seals.

Descriptor	Definition (units)
1. Mean depth (MN_Z)	Mean of all depths recorded during dive (m)
2. Max depth (MX_Z)	Maximum depth recorded during dive (m)
3. Depth variability (Z_CV)	Variability in depth recorded during dive, expressed as the coefficient of variation (CV = standard deviation / mean)
4. Dive duration (DURA_MIN)	Total time spent in dive (min)
5. Total distance (TOT_DIST)	Total distance traveled along the swimming path during dive (m)
6. Mean speed (MN_SPEED)	Mean speed during dive (m s^{-1})
7. Max speed (MX_SPEED)	Maximum speed reached during dive (m s^{-1})
8. Speed variability (SPEED_CV)	Variability in speed during dive, expressed as the coefficient of variation
9. Mean stroking rate (MN_STROKE)	Average number of strokes of hind flippers per second during dive (strokes s^{-1})
10. Maximum stroking rate (MX_STROKE)	Maximum stroking rate during dive (strokes s^{-1})
11. Stroking rate variability (STROKE_CV)	Variability in stroking rate during dive, expressed as the coefficient of variation
12. Total number of strokes (TOT_STROKES)	Total number of strokes of hind flippers during dive (strokes)
13. Total energy (TOT_ENERGY)	Total amount of energy used during dive (ml 0_2 kg^{-1}), calculated using non-feeding equation from Williams et al. (2004)
14. Energy flux (ENERGY_FLX)	Total amount of energy used during dive divided by the amount of time spent in dive (ml 0_2 kg^{-1} min^{-1})
15. Sum of time gliding (SUM_GLIDE)	Total amount of time spent gliding during dive (s)
16. % Time gliding (PCT_GLIDE)	Percentage of entire dive spent gliding
17. Time below 155 m (SUM_155)	Amount of time spent below 155 m, the average minimum depth of silverfish (s)
18. % Time below 155 m (PCT_155)	Percentage of total dive duration spent below 155 m, the average minimum depth of silverfish

Table 3. Jackknife classification results for dives using stepwise discriminant function analysis on 18 variables for the 5-group cluster analysis.

Group	Number of dives	Dives with prey encountered	Jackknife classification					Jackknife classification %
			Group 1	Group 2	Group 3	Group 4	Group 5	
1	44	33	42	0	0	2	0	96
2	46	0	0	43	1	0	2	93
3	41	1	0	2	38	0	1	93
4	74	61	1	0	1	71	1	95
5	29	6	2	1	0	0	26	90

Table 4. Standardized canonical coefficients for all dive descriptors included in the stepwise discriminant function analysis. Variables and coefficients in bold are those that contributed most to the discrimination of dive groups on each discriminant axis.

Descriptor	DA1	DA2
% Dive below silverfish depth	**1.25**	**1.05**
Time below silverfish depth	**-0.83**	**-1.52**
Mean depth	**0.74**	**0.55**
Total energetic cost	**0.68**	**1.01**
Dive duration	**0.60**	**-0.49**
Maximum depth	**-0.53**	-0.38
Total number of strokes	**0.48**	**-0.90**
Mean stroking rate	**0.42**	**0.69**
Speed variability	-0.22	0.00
Total distance	0.19	0.35
Maximum speed	0.17	-0.36
% Dive gliding	-0.16	-0.29
Depth variability	0.13	0.14
Energy flux	-0.11	-0.06
Mean speed	-0.10	0.03
Maximum stroking rate	-0.09	0.21
Sum time gliding	-0.07	-0.18
Stroking rate variability	0.02	0.37

Table 5. Summary statistics (mean ± SE) for five dive groups. Dive descriptors in bold are those which contributed most to the separation according to the stepwise discriminant function analysis.

Descriptor	Non-foraging		Foraging		
	Group 2	Group 3	Group 1	Group 4	Group 5
Mean # prey encountered per dive	0.0 ± 0.0	0.0 ± 0.0	7.8 ± 0.9	16.5 ± 1.3	7.7 ± 2.6
% Dive below silverfish depth	**0.0 ± 0.0**	**0.3 ± 0.3**	**63.4 ± 1.5**	**52.8 ± 2.6**	**14.6 ± 3.5**
Time below silverfish depth (s)	**0.0 ± 0.0**	**1.3 ± 1.3**	**1016.0 ± 30.1**	**482.2 ± 26.0**	**168.3 ± 42.2**
Mean depth (m)	**13.1 ± 1.8**	**31.8 ± 3.4**	**196.6 ± 5.6**	**176.2 ± 6.2**	**81.9 ± 5.7**
Total energetic cost (ml O_2 kg^{-1})	**11.4 ± 1.13**	**25.0 ± 2.11**	**101.74 ± 2.98**	**68.56 ± 1.69**	**57.91 ± 3.40**
Dive duration (min)	**4.1 ± 0.4**	**6.0 ± 0.5**	**27.0 ± 0.7**	**15.6 ± 0.4**	**17.1 ± 0.8**
Maximum depth (m)	**23.1 ± 3.0**	**59.2 ± 5.9**	**331.6 ± 9.9**	**305.2 ± 10.5**	**158.8 ± 9.0**
Total number of strokes (strokes)	**61.9 ± 7.0**	**297.7 ± 26.4**	**1079.9 ± 41.9**	**837.1 ± 21.0**	**523.0 ± 42.6**
Mean stroking rate (strokes s^{-1})	**0.27 ± 0.02**	**0.84 ± 0.03**	**0.67 ± 0.02**	**0.90 ± 0.01**	**0.50 ± 0.02**
Speed variability	0.23 ± 0.01	0.18 ± 0.01	0.19 ± 0.01	0.14 ± 0.01	0.22 ± 0.02
Total distance (m)	269.3 ± 29.9	561.4 ± 54.6	2264.1 ± 79.4	1449.6 ± 35.6	1250.8 ± 75.9
Maximum speed (m s^{-1})	1.88 ± 0.13	2.28 ± 0.11	2.81 ± 0.21	2.44 ± 0.12	2.20 ± 0.16
% Dive gliding	57.7 ± 2.8	15.1 ± 1.7	19.6 ± 1.7	10.0 ± 0.8	37.3 ± 2.0
Depth variability	0.55 ± 0.02	0.63 ± 0.03	0.53 ± 0.01	0.54 ± 0.01	0.64 ± 0.02
Energy flux (ml O_2 kg^{-1} min^{-1})	2.80 ± 0.04	4.15 ± 0.07	3.77 ± 0.04	4.34 ± 0.03	3.35 ± 0.06
Mean speed (m s^{-1})	1.06 ± 0.03	1.54 ± 0.05	1.39 ± 0.02	1.57 ± 0.03	1.20 ± 0.03
Maximum stroking rate (strokes s^{-1})	1.29 ± 0.04	1.77 ± 0.07	1.78 ± 0.05	2.05 ± 0.04	1.68 ± 0.06
Sum time gliding (s)	151.4 ± 17.1	58.3 ± 9.1	309.5 ± 25.4	91.0 ± 6.8	374.4 ± 23.3
Stroking rate variability	1.63 ± 0.08	0.59 ± 0.03	0.73 ± 0.03	0.52 ± 0.01	0.99 ± 0.04

Table 6. Results of contingency table analysis. There were significant differences ($P < 0.001$) in the distribution of dive types at the three different regions. Standardized deviates were used to determine whether and how expected frequencies differed from observed frequencies. Bold standardized deviates indicate which dive types occurred significantly more (> 1.96) or less (< -1.96) frequently than expected by chance.

Dive Group	Observed Frequency			Expected Frequency			Standardized Deviates		
	Erebus	Tent Island	Offshore	Erebus	Tent Island	Offshore	Erebus	Tent Island	Offshore
1	2	37	5	3.6	22.1	18.3	-0.8	**3.2**	**-3.1**
4	9	12	53	6.0	37.3	30.7	1.2	**-4.1**	**4.0**
5	1	25	3	2.4	14.6	12.0	-0.9	**2.7**	**-2.6**

Figure 1. Map of study area within McMurdo Sound with primary diving locations circled and labeled. Seals 19 and 20 dove at Erebus. Seals 25 – 31 dove along the west coast of Tent Island. Seals 25 and 26 dove offshore.

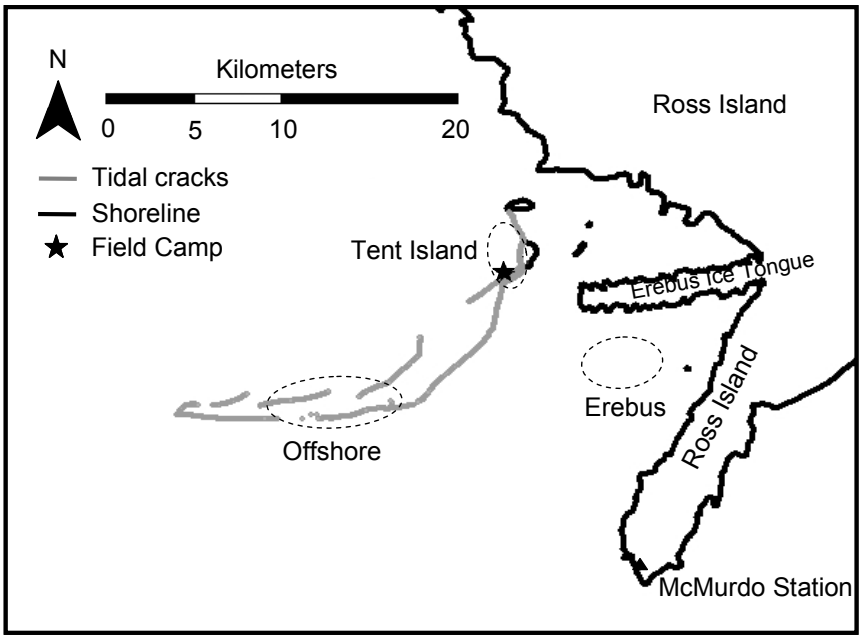


Figure 2. Images captured from the head-mounted video camera. Weddell seals encountered several types of prey while foraging within McMurdo Sound, Antarctica: (a) silverfish (*Pleuragramma antarcticum*) caught in midwater, (b) *Trematomus* spp. encountered on the bottom, (c) bald notothen (*Pagothenia borchgrevinki*) encountered near the surface, and (d) octopus encountered on the bottom. The seal's muzzle and eyes are visible in the lower portion of each image.

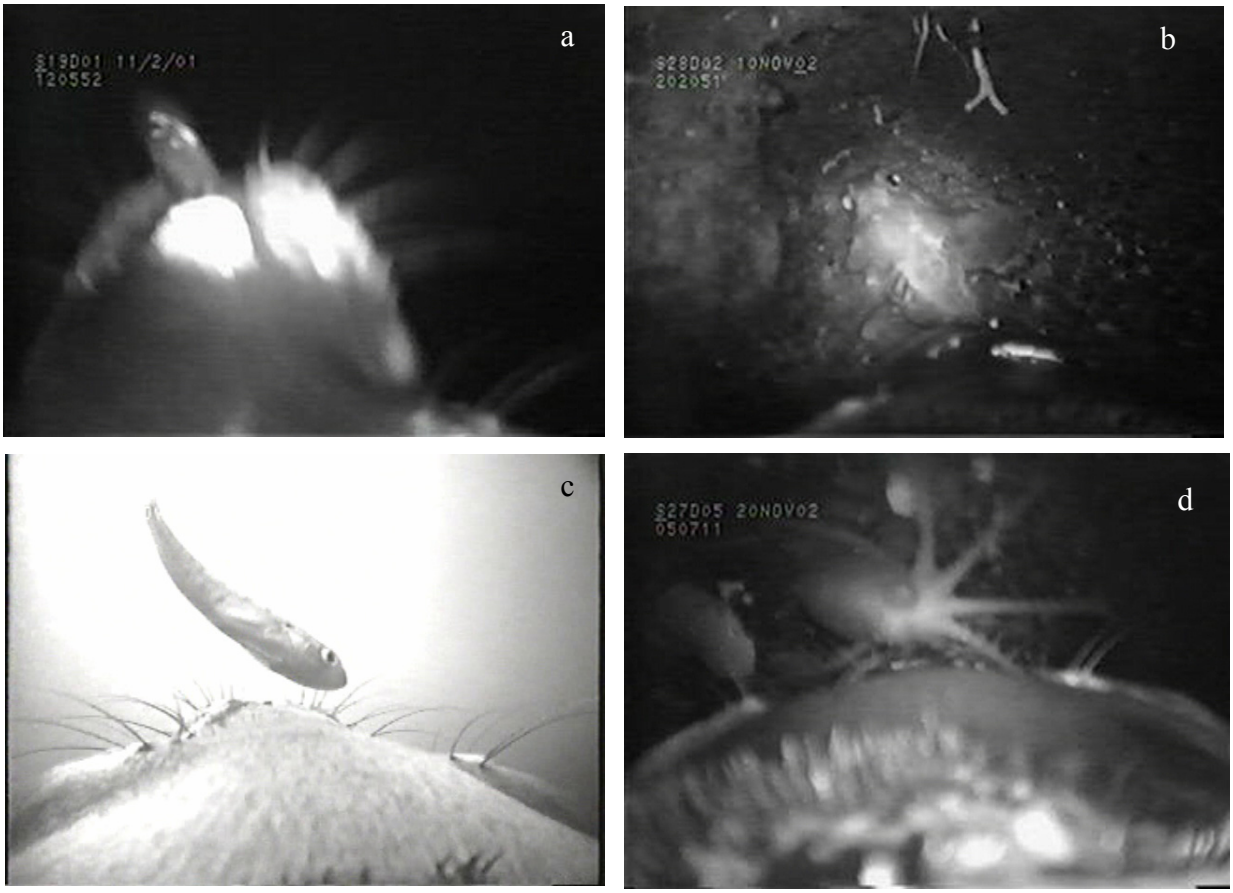


Figure 3. Results of stepwise discriminant function analysis using 5 dive groups that were identified by a *k*-means cluster analysis. (a) View of the discriminant scores for discriminant axes 1 and 2. Points represent individual dives, and symbols identify dive groups. Filled symbols indicate dives in which prey were recorded on the video record. (b) Vector plot of standardized canonical coefficients for discriminant axes 1 and 2. Only those coefficients identified as important in the discrimination are included.

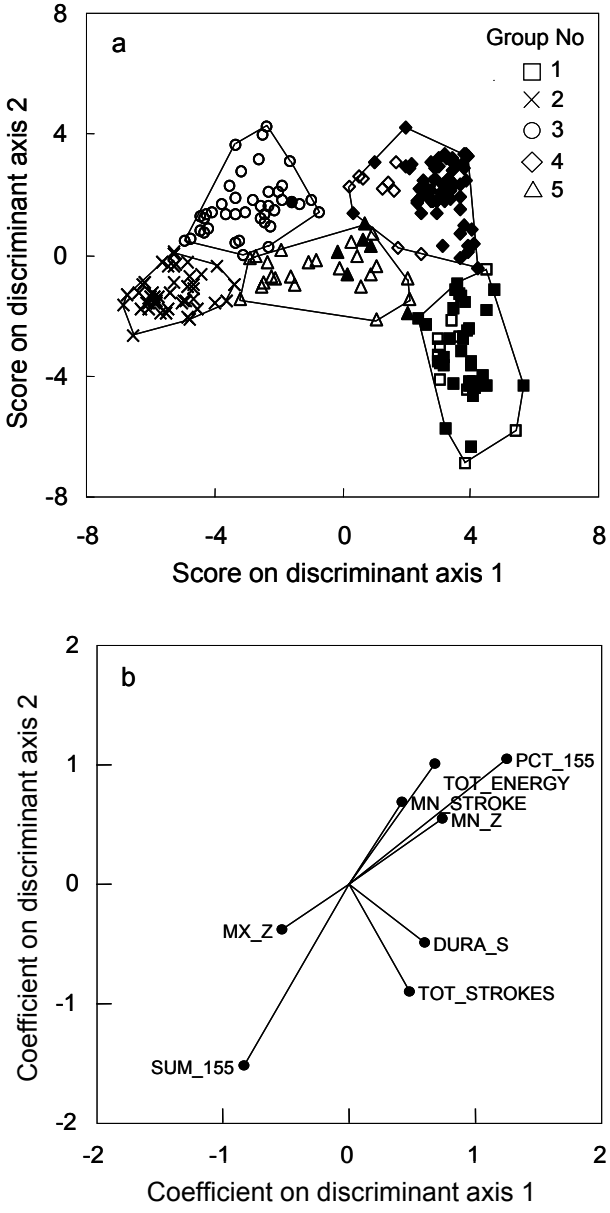


Figure 4. Representative time-depth profiles for each foraging group: (a) Group 1 (deep anaerobic), (b) Group 4 (deep aerobic), and (c) Group 5 (shallow aerobic).

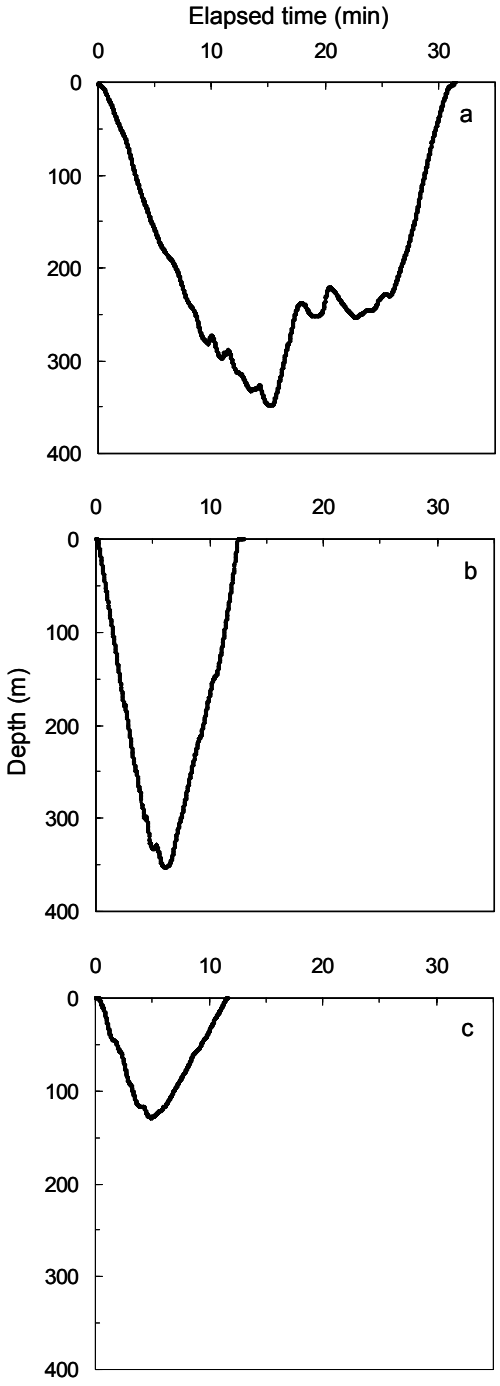


Figure 5. (a) Mean number (± SE) of prey encounters per dive and (b-i) mean values (± SE) for eight dive descriptors which contributed strongly to the separation of dives groups according to discriminant function analysis. Bars are filled according to foraging group (▒ Group 1, ■ Group 4, □ Group 5). Dotted line indicates the available oxygen stores for an average Weddell seal (67 ml O_2 kg^{-1}; Kooyman, 1989).

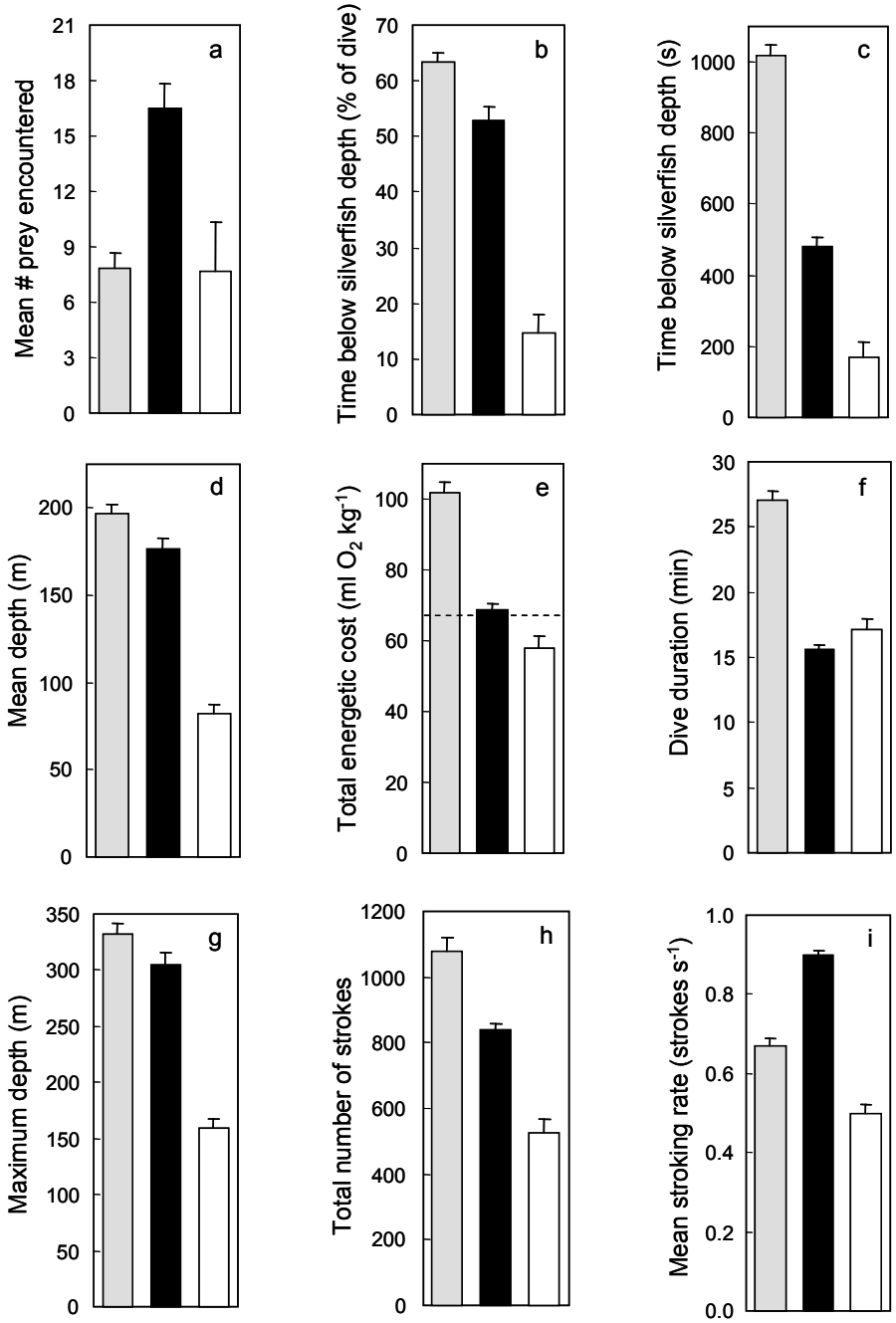
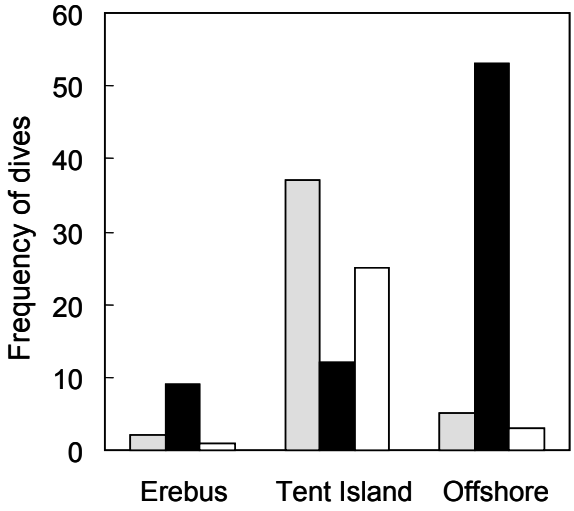


Figure 6. The distribution of foraging dive types was significantly different at the three geographic regions within McMurdo Sound, Antarctica (Pearson's chi-square = 70.0, $P < 0.001$). Bars are filled according to type of foraging dive, (▒ Group 1, ■ Group 4, □ Group 5).



Chapter 3: Individual variability in foraging behavior and success of free-ranging, female Weddell seals

ABSTRACT

Individual variability in foraging behavior has recently arisen as an important topic regarding the ecology of large aquatic predators. Novel techniques allow researchers to record the underwater behavior of large marine predators and gather detailed information about the foraging behavior of individuals. The objectives of the current study were to determine the degree to which foraging behavior and foraging success (defined as number of prey encountered per dive) of a diving predator varies among individuals, and to determine whether such variation in foraging behavior influences the success of the predator. From October to November of 2002, seven adult female Weddell seals (*Leptonychotes weddellii*) were equipped with an animal-borne video camera and data logger, and were allowed to dive freely in McMurdo Sound, Antarctica. Eighteen behavioral descriptors were used to characterize the time, depth, distance, speed, stroking, gliding, and energetic cost of 135 foraging dives. Seals differed significantly in foraging behavior and the number of prey encountered per dive at two locations (coastline and offshore). Behavioral variability was not related to foraging success when prey were easier to access at offshore breathing holes. When the seals began dives on the coastline of an island (shallow bathymetry where midwater prey were more difficult to reach), depth, distance, duration, and energetic cost were related to foraging success. However, the relationship between diving behavior and success varied among individuals. Results also showed that characterization of foraging behavior of individuals requires sampling of a larger number of dives per seal than the number of seals required to characterize the foraging behavior of a group of seals. The current study

indicates that foraging success of Weddell seals is significantly related to behavior, but only in locations where limited access to oxygen requires seals to travel great distances to reach prey. It also illustrates how variability in this relationship can affect the foraging efficiency of individuals. In locations where prey were more accessible and abundant, differences in behavior were not related to foraging success. However, individual variability may become more important in this location if prey abundance changes. Therefore, it is important that individual variability be considered when modeling community- and population-level food-web dynamics and predicting how predators will respond to potential changes in prey abundance.

INTRODUCTION

Foraging behaviors vary among individuals within a population or species, and such variation may have an effect on a predator's ability to locate and capture food (e.g., McLaughlin and Grant, 1994; Ishikawa and Watanuki, 2002; Austin et al., 2006). Behavioral variability can result from extrinsic and intrinsic factors. Extrinsic factors, such as the presence of conspecifics, risk of predation, and changes in prey abundance, location, and quality, can influence the foraging strategies used by individuals (e.g., Oaten, 1977; Stephens and Krebs, 1986; Gese et al., 1996). Intrinsic factors, such as sex, age, body condition, and reproductive status, have also been shown to affect the foraging behavior of individuals (e.g., LeBoeuf et al., 1993; Burns et al., 1997; Stokke and du Toit, 2000). Although these factors produce variability within populations and species, researchers have traditionally focused on the description and analysis of central tendencies, often ignoring the variation among individuals and the consequences of this variability. Examination of interindividual variability is an important analytical tool for understanding physiological and behavioral mechanism and adaptation (Bennett, 1987).

Studies on the diving behavior of marine mammals have focused on average and maximal diving capabilities (e.g., Gentry and Kooyman, 1986; Kooyman, 1989; LeBoeuf et al., 1989). More recent studies have compared the foraging behaviors of marine mammals based on sex, season, year, time of day, prey availability, or geographic location (e.g., Boyd et al., 1994; LeBoeuf et al., 1993; Mattlin et al., 1998). Variation in diving behavior among individuals has received less attention, but has been observed in several species (e.g., Boyd et al., 1991; Burns et al., 1997; Austin et al., 2004). The majority of these studies hypothesized that individual behavioral variability was the result

of potential large-scale variations in prey type, abundance, or distribution that were associated with differences in foraging habitat.

The challenges associated with recording the underwater movements of diving marine predators have made it difficult to determine the amount of variability that exists in foraging success and behavior (Block, 2005). However, new developments in bio-logging technology (i.e., the use of animal-borne instruments to gather data on behavior) have allowed researchers to record prey-related events (e.g., Davis et al., 1999; Plötz et al., 2001; Miller et al., 2004; Austin et al., 2006) and track the movements of diving marine predators in three-dimensions (e.g., Wartzok et al., 1992; Wilson et al., 1991; Mitani et al., 2003).

Weddell seals (*Leptonychotes weddellii*) diving in McMurdo Sound, Antarctica are a good model for testing hypotheses about individual variability in foraging behavior. Their diving behaviors and physiology have been well-studied using time-depth recorders and satellite-linked time-depth recorders (e.g., Kooyman, 1981; Castellini et al., 1992; Plötz et al., 2001), acoustic tracking (Harcourt et al., 2000; Hindell et al., 2002), dead reckoning (Davis et al., 1999, 2003), and geomagnetic and acceleration recorders (Mitani et al., 2003, 2004). Previous studies have shown that age, body mass, body oxygen stores, condition, and sex have the potential to affect diving performance in Weddell seals (Kooyman et al., 1980; Ponganis et al., 1993; Burns and Castellini, 1996; Burns and Testa, 1997; Burns et al., 1997), but very few studies have examined individual variability in foraging behavior, and none have examined individual variability in foraging success. Mitani et al. (2003) used geomagnetic and acceleration recorders to record the three-dimensional movements of two adult seals and found significant differences in the dive headings of the animals. They concluded that the seals used different foraging areas. However, the researchers' equipment could not confirm

foraging events; a foraging function for the dives could only be inferred from other dive data. Fuiman et al. (2007) also recorded the three-dimensional movements of adult Weddell seals but was also able to record foraging events by placing a video camera on the seal's head. They described the structure of foraging dives as a series of behavioral states and prey-related events and found no differences between individuals in either the characteristics (e.g., duration, depth, speed, energetic cost) of behavioral states or the sequence of states within a foraging dive (Fuiman et al., 2007). However, seals in that study were isolated from other seals and restricted to a single breathing hole at a location selected by the researchers. The inability to interact with other seals and travel to other locations could have limited the seals' behavioral repertoire.

In the current study, six adult Weddell seals were equipped with the same video and data recorder (VDR) used by Fuiman et al. (2007). Unlike the previous study, the animals could move freely throughout McMurdo Sound. The objectives were to determine (1) the degree to which foraging behavior and foraging success of Weddell seals varies among individuals, and (2) whether variation in foraging behavior influences the number of prey encountered during a dive. We found significant variation among individuals in foraging behavior and success. We also found that behavioral variability had an effect on the number of prey encountered. When seals began their foraging dives in areas of shallow bathymetry where prey were more difficult to reach, foraging success was affected by variability in dive depth, distance, duration, and energetic cost.

METHODS

Animal capture and instrumentation

We captured six non-lactating, female Weddell seals of similar body mass (463.5 ± 56.5 Kg [mean ± SD]) and standard length (242.0 ± 8.6 cm) near Ross Island,

McMurdo Sound, Antarctica (77º 41' 43.4" S, 166º 20' 4.3" E; Figure 7) from October to November of 2002. Capture and instrumentation methods were fully described by Davis et al., (1999). Briefly, seals were captured on the sea ice using a purse-string net and were transported to a field camp using a specially designed sled. Upon arrival at the field camp, animals were sedated (ketamine and diazepam), weighed, and measured. After cleaning the fur with acetone, a piece of thin neoprene rubber was glued to the seal's back using contact cement. The neoprene rubber provided a secure but flexible attachment for the VDR. The main housing of the VDR was placed in a molded, non-compressible foam cradle and secured to the neoprene rubber with a hose clamp, Velcro, and plastic cable ties. The foam cradle offset the weight of the instruments in water so the unit was neutrally buoyant. The video camera (mounted on the head), compass housing (placed behind the main housing), and accelerometer (located near the base of the tail) were glued to the fur using the same method. A satellite transmitter and two VHF radio transmitters were also glued to the fur to enable us to relocate the seals once they were released. Each animal was allowed to recover from anesthesia for about 18 h before it was released into a 1.3-meter diameter man-made breathing hole at the field camp.

The instruments were typically deployed for 3-5 days before the seals were relocated and had their instruments changed for additional deployments (1-6 deployments per seal). When the seals hauled out on the ice, the satellite transmitters provided the seal's location to within one-half km radius, and VHF radio transmitters enabled us to determine the seal's exact location using a receiver and directional antenna. All animal-handling procedures were in accordance with animal use protocols of The University of Texas at Austin and Texas A&M University.

Equipment

The VDR was designed to record the behavior, swimming performance, three-dimensional movements, and environment immediately in front of diving animals, and has been fully described by Davis et al. (1999). To summarize, the data logger was placed inside a torpedo-shaped, aluminum housing and placed in a non-compressible foam cradle on the animal's back. The data logger recorded data from several instruments: (1) a low-light sensitive black and white video camera mounted on the animal's head and surrounded by an array of infrared light-emitting diodes (LEDs), (2) a pressure transducer, (3) a water speed sensor (paddle wheel), (4) a gimballed flux-gate compass, and (5) a small 1-axis accelerometer placed on the dorsal surface near the seal's tail. The transducers for pressure, speed, and bearing were sampled once per second, while the accelerometer was sampled 16 times per second, and the video recorded at 30 frames per second. The LEDs enabled the camera to record images up to a distance of 1 m at depths where ambient light was less than the threshold level for video recording. When additional ambient light was available, objects were visible at much greater distances. The infrared light source (λ_{max} = 850 nm) was believed to be invisible to the seals and their prey (Lavigne et al., 1977), which prevented any alterations in normal behavior of seals or their prey due to the presence of artificial light. The pressure transducer was calibrated in the laboratory for water depth. The compass was calibrated at the deployment site using the position of the sun together with GPS location, time, and a navigation computer. The speed sensor was calibrated after each deployment using the method of Blackwell et al. (1999). Although it is difficult to determine with certainty the effect of the equipment on the behavior of the animal, the additional hydrodynamic drag created by the VDR did not result in significant differences in the recovery oxygen consumption for seals diving with and without the equipment (Williams et al., 2004).

The frontal area of the video camera and data logger occupied < 5.5% of the frontal area of the seal. Also, the seals continued to feed successfully while carrying the equipment, which suggests that the instrumentation did not have a detrimental effect on foraging behavior.

In order to determine where the seals were diving within McMurdo Sound, the GPS locations of several breathing holes within the study area were gathered using handheld GPS units, and distinct floating markers were placed in each hole so they could be identified on the video record and matched to the handheld GPS coordinates. When the seals failed to surface in a marked hole, distinctive underwater features (e.g., continental slope of Tent Island, the Erebus Ice Tongue) on the video record were used to place the seals within a general geographic context.

Data analysis

Data and video were downloaded immediately upon recovery of the instruments. Each video tape was duplicated in VHS format and a time code was superimposed on the video display to facilitate later analysis. The video tapes were reviewed for scenes of interest (e.g., encounters with prey, substrate visible, hole markers) which were used to build a database of observations. Interactions with several types of prey were documented, including encounters with silverfish, *Trematomus* spp., bald notothen (*Pagothenia borchgrevinki*), icefish, squid, octopus, krill, and several unidentifiable prey items. The number of prey encountered was recorded for every dive and referred to as *total number of encounters*. Eighteen dive descriptors (defined in Table 2), summarizing the time, distance, speed, stroking of the hind flippers, gliding (defined as any period of three or more seconds without hind-flipper stroking), and energetic cost of each dive, were calculated and used to describe foraging behavior. Energetic cost was calculated for each dive from the equation provided by Williams et al. (2004) for non-feeding Weddell

seals. This equation estimates oxygen consumption during a dive from the seal's body mass, duration of the dive, and the number of strokes of the hind flippers during the dive. It does not take into account the added cost associated with processing a meal (i.e., heat increment of feeding), but was chosen because it provided a standard method for calculating energy consumption throughout the entire course of a dive. Energy flux (mL O_2 kg^{-1} min^{-1}) was calculated by dividing the total energetic cost (mL O_2 kg^{-1}) of a dive by dive duration.

The seals performed 200 dives (ranging from 9 to 60 dives per seal) during the 2002 field season. Only the 135 dives (ranging from 7 to 51 dives per seal) identified in Chapter 2 as foraging dives were included in the current analysis (Table 7). The seals were all instrumented and released in the same location, but upon release, the seals were free to travel throughout McMurdo Sound and choose their foraging location. The seals we studied foraged in two locations. All six seals dove at breathing holes along the western coastline of Tent Island, near the release point, and two of the six seals (Seals 25 and 26) traveled away from the coastline and also dove at offshore breathing holes located over deeper water (Figure 7, Table 7). We analyze dives at these locations separately in order to control for potential spatial differences in prey abundance.

Individual variability

Seals were compared for differences in foraging success using the variable total number of encounters (i.e., sum of prey encounters for an each dive). Analysis of similarity (ANOSIM) was used to compare mean foraging success of seals diving along the coastline of Tent Island. ANOSIM was chosen because of the large number of dives in which no prey were encountered (i.e., zero values), which violated the assumption of normality for parametric statistical tests. ANOSIM is the non-parametric equivalent of analysis of variance test (ANOVA) and tests for differences between groups using a

permutation method on a rank similarity matrix (Clarke and Warwick, 2001). Pairwise comparisons were also made to determine differences among individuals. At the offshore breathing holes, total number of encounters was normally distributed with few zeros and a Student's t-test was used to compare Seals 25 and 26 for differences in average foraging success at that location. The ANOSIM was conducted using Primer statistical software (version 6.0, Plymouth Marine Lab), while all other analyses were conducted with Systat statistical software (version 10.2; Systat Software Inc.).

Eighteen dive descriptors (italicized throughout the text, see Table 8) were included in a stepwise discriminant function analysis to determine if seals differed significantly in foraging behavior. Stepwise discriminant analysis was also used to determine which variables were important for discriminating between seals. Wilks' lambda values were used to determine significance, and jackknife classification percentages were examined as an indication of the strength of differences between seals. Variables were considered important in the discrimination if the absolute value of the standardized canonical coefficient was large relative to the remaining scores for that discriminant axis. Separate analyses were performed on each location using the raw data and a tolerance level of 0.001 to add or remove variables from the analysis.

A combination of principal components analysis (PCA) and analysis of covariance (ANCOVA) was used to explore the relationship between foraging behavior, foraging success, and individual variability. Separate PCAs were used for each location to summarize the relationships among the 18 dive descriptors. Variables were considered important on a principal component if the absolute value of the varimax rotated factor loading was large relative to the remaining loadings for that principal component. Principal components that had eigenvalues greater than 1.0 and that also explained a large percentage of the variance were included as factors in the ANCOVAs. Four ANCOVAs

were conducted, one for each important principal component at each location. Foraging success (expressed as log[total number of encounters + 1]) at Tent Island and total number of encounters offshore), was compared among seals, with the principal component scores as covariates.

RESULTS

The video record showed that prey were encountered in both locations (western coastline of Tent Island and offshore) throughout the length of our study. Seals were able to locate prey regardless of any changes in prey abundance or location that may have occurred. Silverfish was the primary component of the seal's diet along the western coastline of Tent Island and at the offshore breathing hole (95.2 and 99.6% of the diet, respectively). There was no significant difference between the two locations in the depth of the first silverfish encounter (Student's t-test, $P = 0.431$), but there was a significant difference in the time to the first encounter in a dive (Student's t-test, $P < 0.001$). Seals encountered the first silverfish in a dive significantly earlier at the offshore breathing holes (5.8 ± 0.2 min) than they did at Tent Island (10.6 ± 0.5 min).

Foraging success

There were significant differences among seals diving at Tent Island in the mean total number of encounters (Figure 8a; ANOSIM, $R = 0.11$, $P = 0.001$). Seal 26 never encountered prey at this location and differed significantly from all other seals, except Seal 31 (mean number of encounters ± SE: 1.4 ± 1.1). Seals 25 and 29 were also relatively unsuccessful (1-2 encounters per dive), and Seal 29 differed significantly from Seals 27 and 28, the two most successful seals (7.4 ± 1.8 and 4.9 ± 1.5 encounters per dive, respectively). The two seals diving offshore encountered more prey than those diving on the coast and they were significantly different from one another in foraging

success (Figure 8b; Student's t-test; $P < 0.005$), with Seal 26 being more successful (19.6 ± 0.8) than Seal 25 (12.8 ± 0.8).

Foraging behavior

Stepwise discriminant analysis eliminated only one dive descriptor from the analysis, total energetic cost. Based on the 17 remaining dive descriptors, the behavior of seals diving at Tent Island was significantly different from one seal to another (Wilks' lambda = 0.012, $P < 0.001$). Jackknife classification percentages indicated a relatively strong degree of separation between the seals, with an overall classification success of 64% (values ranged from 43 – 81% for individual seals). The first four discriminant axes (DA1, DA2, DA3, DA4) were useful in discriminating between individual seals (eigenvalues 2.8, 2.3, 1.6, 1.0, respectively) (Figure 9). Variables summarizing movements of the hind flippers, distance traveled, depth, and swimming speed loaded heavily on DA1 and DA2 (Tables 9 & 10). Variables describing the duration, distance traveled, stroking rate, energy flux, and amount of gliding were important along DA3 and DA4 (Tables 9 & 10). DA5 did not contribute to the overall separation of seals (eigenvalue of 0.2).

When diving at the offshore breathing holes, Seals 25 and 26 were significantly different from one another in foraging behavior (Wilks' Lambda = 0.121, $P < 0.001$). Jackknife classification percentages indicated a very strong degree of separation between the two seals with overall classification success of 97%. The absolute values of the standardized canonical coefficients for DA1 showed that the total distance traveled and the amount of variability in the stroking rate were very important for discriminating between the two seals (Tables 9 & 11).

Foraging success and behavior

At Tent Island, PCA produced two principal components with eigenvalues greater than 1.0. Principal component 1 (PC1) and PC2 explained 70.5% of the total variance. Five descriptors describing the stroking or gliding (i.e., lack of stroking) and two descriptors describing speed and energy flux had high loadings on PC1 (Table 12). PC1 explained 47.0% of the variance and primarily described the locomotor activity within a dive. PC2 emphasized descriptors that characterized the depth of a dive, and to a slightly lesser extent the overall magnitude of the dive, and explained 23.5% of the total variance (Table 12). At the offshore breathing holes, PCA produced five principal components with eigenvalues greater than 1.0. However, PC1 and PC2 explained the majority of the total variance (61.1%). When combined, PC3, PC4, and PC5 explained an additional 26.8% of the total variance (12.1, 8.1, and 6.7%, respectively). As in the PCA for Tent Island, PC1 reflected energetic cost and locomotor activity through stroking and gliding (Table 13) and explained 36.7% of the total variance. PC2 explained 24.4% of the total variance and all five variables with high loadings on this axis summarized dive depth (Table 13).

At Tent Island, the relationship between foraging behavior and foraging success, expressed as log(total number of encounters + 1), was compared among seals using the principal components as covariates in the ANCOVAs. Differences in locomotor activity (PC1) among seals did not have a significant effect on foraging success ($F_{1,64} = 1.8$, $P = 0.134$), and there was no overall relationship between locomotor activity and foraging success ($F_{1,64} = 0.8$, $P = 0.368$). However, there were significant differences between individual seals in foraging success ($F_{5,64} = 5.7$, $P < 0.001$). When the depth and magnitude of a dive (PC2) was used as a covariate in the ANCOVA, there were significant differences among seals in the relationship between foraging success and

depth, distance, duration, and energetic cost (Figure 10; $F_{1,64} = 3.8$, $P = 0.005$). This indicates that the number of encounters was explained by depth and magnitude of a dive, but the relationship between success and behavior was different among individuals. The relationship was positive for all seals, except Seal 26 which was always unsuccessful at Tent Island. Seal 28 was the most effective predator at this location, as indicated by the regression line with the highest slope value (Figure 10). Seals 31 and 27 were also good hunters in this region, but Seals 25 and 29 were not as efficient when foraging along the coastline of Tent Island.

At the offshore breathing holes, there was no significant differences between individuals in the relationship between locomotor activity (PC1) and foraging success ($F_{1,57} = 0.2$, $P = 0.689$), and there was no significant overall relationship between locomotor activity and the number of prey encountered ($F_{1,57} = 2.1$, $P = 0.156$). However, there were significant differences between individuals in the number of encounters ($F_{1,57} = 12.0$, $P = 0.001$). When depth (PC2) was included as a covariate in the ANCOVA, similar results were obtained. There were no significant differences between individuals in the relationship of depth (PC2) and foraging success ($F_{1,57} = 0.0$, $P = 0.876$) and no significant overall relationship with depth ($F_{1,57} = 0.0$, $P = 0.989$), but individual variability did have a significant effect on total number of encounters ($F_{1,57} = 23.3$, $P < 0.001$).

DISCUSSION

Few studies have simultaneously incorporated data on the foraging success and behavior of diving predators (Kato et al., 1996; Davis et al., 1999; Lesage et al., 1999; Ropert-Coudert et al., 2001; Baechler et al., 2002). A recent study by Austin et al. (2006) used time-depth recorders and stomach temperature loggers to record the feeding frequency and foraging behavior of gray seals (*Halichoerus grypus*). They found that the

most important predictor of foraging success at short temporal scales (3 h) was time spent at the bottom of a dive. However, estimated total distance travelled, path tortuosity (calculated as angular variance of mean turning angle), and bathymetry were also significant factors in determining the number of feeding events when longer temporal scales were considered. Feeding varied across temporal scales and environmental variation became important at some scales and not at others. However, they did not attempt to determine the relationship between success and behavior at the level of individual dives and no comparisons were made among individuals. Tinker et al. (2007) was able to simultaneously gather information on the diet and foraging behavior of sea otters on a per dive basis and found that individuals exhibited dietary specialization, aggregating into one of three distinct dietary groups. They also found that dietary specialization was reflected in dive parameters and that time-depth profiles could be used to classify individuals into dietary groups.

Significant differences were found in foraging success and foraging behavior among Weddell seals diving at two locations within McMurdo Sound. However, significant relationships between behavior and foraging success were found only for seals diving along the western coastline of Tent Island. In this location, there was a positive relationship between the total number of prey encountered and the depth and magnitude of a dive (PC2). In other words, dives that were deeper, of longer duration, covered a greater distance, and had a higher energetic cost contained more prey encounters. This relationship was due to the combination of the bathymetry along the coastline of Tent Island and the location of silverfish, the main prey of Weddell seals in McMurdo Sound (Castellini et al., 1992; Burns et al., 1998). The spatial and temporal distribution of prey has a strong effect on the energetic cost of foraging, foraging success, and overall predator survival (Boyd, 1996). Silverfish in McMurdo Sound reside at depths of 252-

346 m, depending on time of day (Fuiman et al., 2002). When diving along the coastline, the seals were restricted by the shallow bathymetry and were forced to travel farther in the horizontal plane in order to reach the depth where silverfish were located (mean minimum depth of 155 m). As a result, the first encounter did not occur until late in a dive (10.6 ± 0.5 min). In contrast, the first prey encountered for the two seals diving offshore, where bathymetry did not constrain descent rate, occurred 5.8 ± 0.2 min after the start of the dive. Diving longer and traveling a greater distance, which incurs a greater energetic cost, would therefore increase a seal's chance of encountering silverfish and explains the positive relationship between success and dive depth, distance, duration, and energetic cost at Tent Island. A previous study by Mitani et al. (2004) found similar results for Weddell seals diving at two colonies with varying bathymetry. Both locations were shown to have a large abundance of prey at similar depths (Watanabe et al., 2003), but the slope of the island prevented the seals at one colony from descending steeply so the seals at the first colony had to travel much farther to reach prey than the seals at the second colony (Mitani et al., 2004).

Although behavior had a significant effect on foraging success at Tent Island, the relationship between success and depth, distance, duration, and energetic cost differed among seals. This indicates that some seals were inherently more successful when diving along the coastline than other seals. This has important implications for the foraging efficiency (ratio of energy gained to energy expended), energy budgets, and ultimately, the fitness level of the seals diving along the coastline of Tent Island. When the energetic costs associated with traveling to, and foraging at, the depths where prey are located are high, such as along the coastline, differences between individuals may be particularly important. In fact, the estimated energetic cost of foraging at Tent Island exceeded the calculated available oxygen stores of an average adult Weddell seal (67 ml O_2 kg^{-1}

[Kooyman, 1989]) for all but one seal (Table 10), indicating that seals may have used anaerobic metabolism when foraging in this location. If seals devote similar amounts of time and energy to foraging but some individuals catch fewer prey, the foraging efficiency of these individuals is going to be lower.

Only two seals travelled away from Tent Island and dove at breathing holes located over the deeper waters of McMurdo Sound. Those two seals were significantly different from one another in foraging success and behavior when diving offshore, but unlike the seals diving at Tent Island, the differences in foraging success were not explained by differences in behavior. Seals 25 and 26 were much more successful when foraging at the offshore breathing holes than they were at Tent Island. Seal 25 averaged less than two encounters per dive at Tent Island, but caught an average of almost 13 prey per dive at the offshore breathing holes. Seal 26 was unsuccessful in all 16 dives along the coastline, but averaged almost 20 encounters per dive at the offshore breathing holes. When diving offshore, the seals were not constrained by bathymetry and were able to travel more quickly to the depths where silverfish were located, leaving more time to forage at depth. Seal 25 expended less energy when diving offshore and encountered more fish, resulting in a greater ratio of energy gained to energy expended for this location. Seal 26 expended a similar amount of energy at the offshore location as it did while diving at Tent Island (Tables 10 & 11) and exceeded its calculated available oxygen stores, but since Seal 26 encountered 20 more prey items while diving offshore, the ratio of energy gained to energy expended was much higher offshore.

In addition to being easier to reach, previous studies have suggested that offshore areas may have a higher abundance of pelagic prey during the summer season since most seals are aggregated near the coastline for breeding (Testa et al., 1985). The combination of easier accessibility and higher abundance of silverfish could explain why behavior and

individual variability did not have a similar effect on foraging success offshore as they did at Tent Island. If prey are easier to access and probably more abundant, seals may be able to use a greater variety of foraging strategies that result in successful capture of prey, and differences between individuals might not be as important as they are at coastal locations. A previous study by Boyd et al. (2001) found a similar pattern for Antarctic fur seals (*Arctocephalus gazella*) diving in the sub-Antarctic near South Georgia Island. Individuals varied in foraging strategy, but all strategies appeared to be equally successful in years when food was plentiful. However, if prey become less abundant offshore, differences between individuals may have an effect on foraging success.

If certain individuals are less efficient when hunting along the coast of Tent Island, why did only two seals travel offshore where silverfish are more accessible and possibly more abundant? One advantage of diving along the coastline is the increased concentration of breathing holes located near Tent Island. The number of breathing holes is more limited offshore, and the difficulty of finding and defending breathing holes in this location may make foraging along the coast preferable, despite the higher cost of foraging (125 and 119% higher for Seals 25 and 26, respectively). When diving animals can surface at any location to breathe, it is easier to move to areas where prey are more abundant and accessible. Without the restrictions imposed by limited access to the surface, such as in ice free areas, individual differences in foraging behavior may be more important in determining success.

Another possible explanation for the seals' preference to remain near Tent Island, despite the fact that some are less efficient hunters (i.e., Seal 29), is the tendency for adult seals to congregate along coastlines during the summer breeding season (e.g., Kooyman, 1968; Castellini et al., 1992; Testa, 1994). Deployments for Seals 25 and 26 were early in the season (Oct 27 – Nov 10), while deployments for Seals 27-31 were slightly later

(Nov 7 – Dec 5). Seals are most congregated in breeding areas during the month of December (Kooyman, 1981), so it may be that foraging took priority during the early part of our study, but mating became more important as the season progressed.

Detailed statistical comparisons of foraging behavior among individuals provide an opportunity for input into the design of future behavioral studies of diving animals. We used our data for seals diving at Tent Island to estimate the number of individuals needed to describe the average foraging behavior of a population of Weddell seals, using the equation:

$$n \geq (z_{0.025}\ s)^2 / B^2$$

where $z_{\alpha/2}$ is a standard normal deviate (1.96), s is the among-seal standard deviation for a dive descriptor, and B is the acceptable bound on the error of the mean (2, 5, and 10% of the observed mean for each descriptor). For the dive descriptor with the maximum number of seals reported (maximum speed), researchers would need to sample dive data from 23 individuals in order to be 95% confident that their results were within 10% of the mean (Table 14). The minimum sample size increases to 93 seals to be within 5% of the true mean, and 582 seals to be within 2%. Minimum sample sizes varied widely among the dive descriptors (Table 14).

The same equation was used to estimate the number of foraging dives needed to characterize the foraging behavior of an individual seal. Here, calculations were based on within-seal standard deviations. For the dive descriptor with the maximum number of dives reported (time below 155 m), researchers would need to collect data from 405 foraging dives in order to be 95% confident that there results were within 10% of the mean. The minimum sample size increases to 1,618 dives and 10,113 dives as the error bound narrows to 5% and 2% of the mean, respectively. Again, minimum sample sizes varied widely among the dive descriptors (Table 14). Based on these results, a large

number of foraging dives must be sampled in order to characterize an individual, indicating that researchers should focus more on collecting a large number of dives from a relatively small number of seals. Since we sampled 7-16 dives per seal, the calculations of the minimum number of seals to observe based on the 10% error bound (Table 8) are more reliable than those for the 2% and 5% error bounds.

Results of this study show that significant behavioral variability can exist among individuals that otherwise appear to be homogenous (i.e., sex, body mass, length, geographic location). We found that variables such as depth, distance, duration, and energetic cost are important for explaining foraging success, but only under certain conditions. When silverfish were more difficult to reach and probably less abundant, behavioral variability had an effect on the number of prey encountered. However, the effect was not the same for all individuals, and some seals were more successful than others, even when using the same type of behavior. Behavioral variability was not as important for explaining success when prey were more abundant and easier to access, as was the case at the offshore breathing holes. Therefore, behavioral plasticity may be particularly important to diving predators when diet breadth is narrow, bathymetry is variable, and access to air is at a distance from their prey.

Our findings suggest that individual variability cannot be ignored when calculating foraging efficiencies of diving predators and that characterization of foraging behavior of individuals requires an emphasis on sampling a large number of dives per seal, rather than concentrating on a larger number of seals. The ability to include foraging behavior plasticity and its effect on foraging success into ecosystem and community models will ultimately improve our understanding of resource utilization and niche breadth (Morse, 1980) and effects of predation pressure (Lima and Dill, 1990; Abrams, 1993) on large marine predators.

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Table 7. Mass, length, and number of foraging dives for six adult, female Weddell seals instrumented from October to November, 2002 in McMurdo Sound, Antarctica. Number of foraging dives is shown for each of the two main diving locations.

			Foraging dives	
Seal No	**Mass (Kg)**	**Length (cm)**	**Tent Island**	**Offshore**
25	391.0	231.5	8	43
26	428.4	246.0	16	18
27	459.2	232.0	16	
28	466.6	245.0	13	
29	559.8	253.5	14	
31	476.0	244.0	7	

Table 8. Descriptors of behavior for 135 foraging dives made by six free-ranging Weddell seals in McMurdo Sound, Antarctica.

Descriptor	Definition (units)
1. Mean depth	Mean of all depths recorded during dive (m)
2. Max depth	Maximum depth recorded during dive (m)
3. Depth variability	Variability in depth recorded during dive, expressed as the coefficient of variation (CV = standard deviation / mean)
4. Dive duration	Total time spent in dive (min)
5. Total distance	Total distance travelled along the swimming path during dive (m)
6. Mean speed	Mean speed during dive (m s^{-1})
7. Max speed	Maximum speed reached during dive (m s^{-1})
8. Speed variability	Variability in speed during dive, expressed as the coefficient of variation
9. Mean stroking rate	Average number of strokes of hind flippers per second during dive (strokes s^{-1})
10. Maximum stroking rate	Maximum stroking rate during dive (strokes s^{-1})
11. Stroking rate variability	Variability in stroking rate during dive, expressed as the coefficient of variation
12. Total number of strokes	Total number of strokes of hind flippers during dive (strokes)
13. Total energy	Total amount of energy used during dive (ml 0_2 kg^{-1}), calculated using non-feeding equation from Williams et al. (2004)
14. Energy flux	Total amount of energy used during dive divided by the amount of time spent in dive (ml 0_2 kg^{-1} min^{-1})
15. Sum of time gliding	Total amount of time spent gliding during dive (s)
16. % Time gliding	Percentage of entire dive spent gliding
17. Time below 155 m	Amount of time spent below 155 m, the average minimum depth of silverfish (s)
18. % Time below 155 m	Percentage of total dive duration spent below 155 m, the average minimum depth of silverfish

Table 9. Standardized canonical coefficients for all dive descriptors included in the stepwise discriminant function analyses for Tent Island and the offshore breathing holes. Variables and coefficients in bold are those that contributed most to the discrimination of dive groups on each discriminant axis.

Descriptor	Tent Island				Offshore
	DA1	DA2	DA3	DA4	DA1
Mean stroking rate	**6.12**	**11.09**	**8.30**	-5.88	-0.19
Total distance	**5.72**	1.34	**-3.92**	-3.59	**-4.87**
Max depth	**-5.52**	-2.82	-0.86	-3.40	-0.32
Mean depth	**4.97**	2.60	0.13	2.20	1.43
Stroking rate variability	**4.38**	-2.28	-2.15	-3.10	**4.46**
Total number of strokes	**-3.41**	-1.34	-1.26	-7.42	2.71
Mean speed	**-3.00**	0.10	1.35	1.74	2.16
Energy flux	0.41	**-12.11**	**-7.20**	7.34	1.94
Dive duration	-1.58	1.17	**5.88**	**12.02**	-0.08
% Time gliding	-0.14	3.01	**4.98**	6.07	-2.45
Sum of time gliding	0.15	-1.19	-2.17	-5.11	1.09
% Time below 155 m	1.42	1.79	-0.38	2.02	-1.94
Time below 155 m	-1.26	-1.67	0.25	-1.96	0.86
Max speed	0.37	-0.24	0.43	-0.63	0.63
Depth variability	1.30	0.45	0.76	0.61	-0.06
Max stroking rate	-0.41	0.18	0.35	0.36	-0.19
Speed variability	-0.28	-0.65	-0.71	0.18	0.31

Table 10. Summary statistics (mean ± SE) for foraging dives by Weddell seals at breathing holes located along the western coast of Tent Island.

Descriptor	Seal 26		Seal 29		Seal 31	
Total number of prey encounters	0.0	± 0.0	1.1	± 0.5	1.4	± 1.1
Mean depth (m)	84.9	± 9.8	161.0	± 14.4	71.7	± 11.8
Max depth (m)	150.5	± 16.8	266.8	± 21.1	139.8	± 20.6
Depth variability	0.55	± 0.03	0.55	± 0.01	0.65	± 0.04
Dive duration (min)	18.7	± 1.7	24.8	± 2.0	16.5	± 1.6
Total distance (m)	1441.4	± 158.1	2170.4	± 209.4	1229.4	± 162.3
Mean speed (m s^{-1})	1.29	± 0.08	1.44	± 0.05	1.22	± 0.05
Max speed (m s^{-1})	2.51	± 0.34	2.33	± 0.19	1.92	± 0.17
Speed variability	0.16	± 0.01	0.19	± 0.02	0.12	± 0.01
Mean stroking rate (strokes s^{-1})	0.71	± 0.05	0.56	± 0.04	0.41	± 0.04
Max stroking rate (strokes s^{-1})	1.75	± 0.08	1.72	± 0.14	1.60	± 0.14
Stroking rate variability	0.75	± 0.07	0.94	± 0.07	1.09	± 0.08
Total number of strokes (strokes)	828.9	± 112.4	851.8	± 106.9	427.4	± 77.7
Total energy (ml O_2 kg^{-1})	73.65	± 7.97	86.99	± 8.20	52.38	± 6.33
Energy flux (ml O_2 kg^{-1} min^{-1})	3.86	± 0.13	3.47	± 0.10	3.13	± 0.10
Sum of time gliding (s)	245.5	± 43.2	446.7	± 44.7	402.1	± 24.0
% Time gliding	24.3	± 4.0	31.9	± 3.8	42.2	± 3.7
Time below 155 m (s)	194.4	± 75.4	831.3	± 124.2	149.6	± 94.6
% Time below 155 m	14.8	± 5.0	52.5	± 6.7	11.6	± 7.1

Table 10. Summary statistics (mean ± SE) for foraging dives by Weddell seals at breathing holes located along the western coast of Tent Island.

Descriptor	Seal 25	Seal 28	Seal 27
Total number of prey encounters	1.5 ± 0.9	4.8 ± 1.5	7.4 ± 1.8
Mean depth (m)	167.2 ± 16.7	161.1 ± 11.4	158.3 ± 12.5
Max depth (m)	270.5 ± 27.9	268.3 ± 19.2	287.0 ± 24.0
Depth variability	0.51 ± 0.02	0.54 ± 0.01	0.54 ± 0.02
Dive duration (min)	24.1 ± 1.5	23.1 ± 1.1	26.4 ± 1.9
Total distance (m)	1851.3 ± 100.7	1823.7 ± 114.8	2326.9 ± 177.4
Mean speed (m s^{-1})	1.29 ± 0.04	1.31 ± 0.03	1.45 ± 0.03
Max speed (m s^{-1})	1.75 ± 0.03	1.91 ± 0.04	3.38 ± 0.29
Speed variability	0.16 ± 0.01	0.16 ± 0.01	0.19 ± 0.02
Mean stroking rate (strokes s^{-1})	0.71 ± 0.06	0.59 ± 0.03	0.71 ± 0.02
Max stroking rate (strokes s^{-1})	1.73 ± 0.03	1.64 ± 0.04	1.89 ± 0.07
Stroking rate variability	0.72 ± 0.06	0.76 ± 0.04	0.61 ± 0.03
Total number of strokes (strokes)	998.0 ± 64.2	820.1 ± 63.0	1131.6 ± 85.9
Total energy (ml O_2 kg^{-1})	93.09 ± 4.97	82.26 ± 4.69	101.96 ± 7.37
Energy flux (ml O_2 kg^{-1} min^{-1})	3.90 ± 0.14	3.55 ± 0.07	3.86 ± 0.05
Sum of time gliding (s)	249.6 ± 62.3	300.1 ± 30.6	191.0 ± 29.3
% Time gliding	17.3 ± 4.2	22.7 ± 2.9	12.5 ± 2.1
Time below 155 m (s)	856.6 ± 140.8	758.5 ± 88.4	785.3 ± 125.7
% Time below 155 m	56.1 ± 8.4	52.2 ± 5.0	44.5 ± 6.5

Table 11. Summary statistics (mean ± SE) for foraging dives by Weddell seals at offshore breathing holes located over the deeper waters of McMurdo Sound.

Descriptor	Seal 26		Seal 25	
Total number of prey encounters	19.6	± 0.8	12.8	± 0.8
Mean depth (m)	196.2	± 3.9	186.6	± 8.4
Max depth (m)	342.0	± 6.0	329.3	± 12.3
Depth variability	0.54	± 0.01	0.56	± 0.01
Dive duration (min)	14.0	± 0.2	17.3	± 0.6
Total distance (m)	1510.2	± 60.7	1439.5	± 35.6
Mean speed (m s^{-1})	1.83	± 0.08	1.42	± 0.01
Max speed (m s^{-1})	2.60	± 0.12	2.70	± 0.23
Speed variability	0.12	± 0.01	0.16	± 0.01
Mean stroking rate (strokes s^{-1})	0.94	± 0.01	0.89	± 0.01
Max stroking rate (strokes s^{-1})	2.00	± 0.06	2.08	± 0.05
Stroking rate variability	0.42	± 0.01	0.53	± 0.01
Total number of strokes (strokes)	771.5	± 14.3	892.4	± 17.2
Total energetic cost (ml O_2 kg^{-1})	61.42	± 0.77	74.35	± 1.95
Energy flux (ml O_2 kg^{-1} min^{-1})	4.41	± 0.04	4.35	± 0.04
Sum of time gliding (s)	57.8	± 5.1	110.3	± 10.2
% Time gliding	6.9	± 0.6	10.1	± 0.7
Time below 155 m (s)	525.6	± 13.7	571.9	± 37.9
% Time below 155 m	62.8	± 1.4	56.1	± 3.1

Table 12. Rotated factor loadings for all dive descriptors included in principal component analysis at Tent Island. Coefficients in bold indicate those variables that are considered important along each principal component (PC).

Descriptor	PC1	PC2	PC3	PC4
Stroking rate variability	**-0.94**	-0.20	0.01	-0.09
Mean stroking rate	**0.93**	0.05	-0.05	0.26
% Time gliding	**-0.93**	-0.27	0.00	-0.12
Energy flux	**0.93**	0.06	-0.07	0.25
Sum of time gliding	**-0.91**	0.19	-0.09	0.16
Total number of strokes	**0.62**	0.58	-0.05	0.44
Mean speed	**0.52**	0.16	-0.03	0.36
Time below 155 m	0.02	**0.98**	0.03	0.09
Max depth	0.04	**0.97**	0.12	-0.04
Mean depth	0.05	**0.96**	0.06	0.02
% Time below 155 m	0.01	**0.94**	0.04	-0.04
Dive duration	0.17	**0.83**	-0.07	0.44
Total distance	0.31	**0.73**	-0.04	0.48
Total energy	0.42	**0.73**	-0.07	0.46
Max speed	0.21	0.13	**0.85**	0.03
Speed variability	-0.41	-0.06	**0.81**	0.00
Max stroking rate	0.09	0.10	0.48	**0.67**
Depth variability	-0.50	-0.09	0.19	**-0.57**

Table 13. Rotated factor loadings for all dive descriptors included in principal component analysis at the offshore breathing holes. Coefficients in bold indicate those variables that are considered important along each principal component (PC).

Descriptor	PC1	PC2	PC3	PC4	PC5
Mean stroking rate	**-0.93**	0.02	-0.06	0.01	-0.15
Sum of time gliding	**0.91**	-0.18	0.02	0.06	0.28
Stroking rate variability	**0.90**	-0.15	-0.04	0.14	0.27
Energy flux	**-0.88**	-0.07	0.04	0.11	0.02
% Time gliding	**0.85**	-0.24	0.06	0.10	0.11
Dive duration	**0.74**	0.14	-0.16	0.00	0.53
Total energetic cost	**0.62**	0.14	-0.14	0.03	0.72
Mean depth	-0.05	**0.97**	0.10	0.00	0.04
Time below 155 m	0.07	**0.94**	-0.04	0.04	0.28
% Time below 155 m	-0.34	**0.89**	0.03	0.01	-0.06
Max depth	-0.18	**0.88**	0.25	0.07	0.06
Depth variability	-0.15	**-0.79**	0.24	0.22	0.04
Max speed	-0.01	0.18	**0.90**	-0.16	-0.12
Speed variability	0.24	0.09	**0.89**	0.07	-0.16
Max stroking rate	0.30	0.22	**-0.58**	-0.05	-0.14
Mean speed	-0.35	0.00	0.03	**-0.88**	-0.28
Total distance	0.35	0.06	0.04	**-0.75**	0.54
Total number of strokes	0.27	0.11	-0.07	0.06	**0.93**

Table 14. Number of seals and foraging dives needed to estimate with 95% confidence the value of each dive descriptor to within 2, 5, and 10% of the mean.

Descriptor	Number of seals			Number of foraging dives per seal		
	2%	5%	10%	2%	5%	10%
Mean depth	41	7	2	1219	195	49
Max depth	40	6	2	1124	180	45
Depth variability	42	7	2	184	29	7
Dive duration	66	11	3	683	109	27
Total distance	127	20	5	981	157	39
Mean speed	41	7	2	189	30	8
Max speed	582	93	23	915	146	37
Speed variability	390	62	16	1369	219	55
Mean stroking rate	69	11	3	575	92	23
Max stroking rate	88	14	4	344	55	14
Stroking rate variability	74	12	3	594	95	24
Total number of strokes	192	31	8	1518	243	61
Total energetic cost	109	17	4	901	144	36
Energy flux	12	2	1	92	15	4
Sum of time gliding	238	38	10	2674	428	107
% Time gliding	139	22	6	2939	470	118
Time below 155 m	301	48	12	10113	1618	405
% Time below 155 m	86	14	3	8493	1359	340

Figure 7. Map of study area within McMurdo Sound with diving locations enclosed by a dashed line. Seals 25 – 31 dove along the west coast of Tent Island, but Seals 25 and 26 traveled away from the coastline and dove offshore.

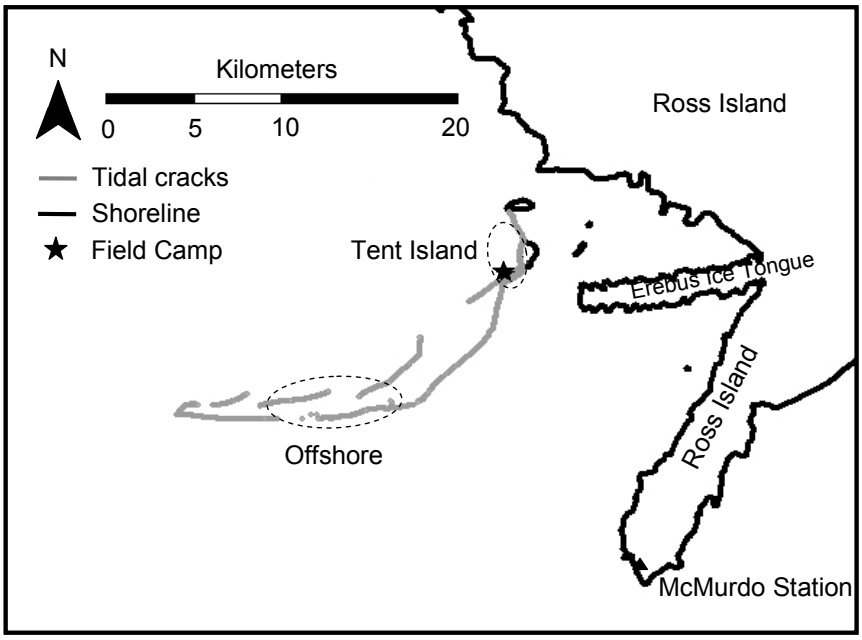


Figure 6. Mean number of prey encounters per dive per seal for seals foraging in two areas within McMurdo Sound. (a) Coastline of Tent Island (b) Offshore. Letters above bars reflect results of pairwise comparisons. Bars that share a common letter are not significantly different ($P < 0.05$).

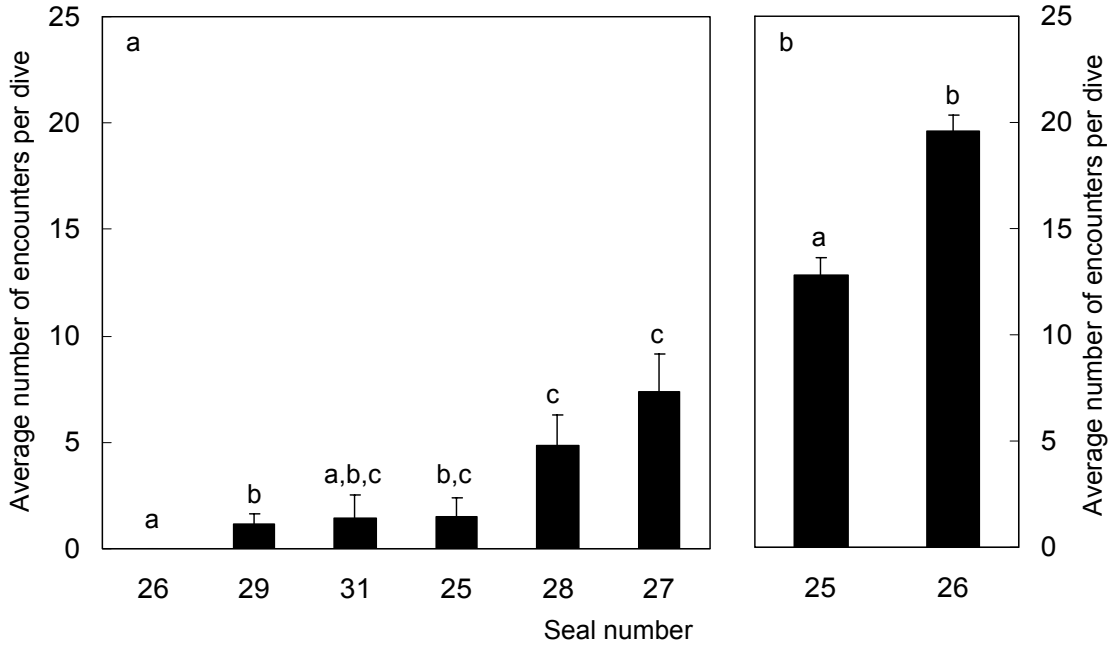


Figure 8. Results of stepwise discriminant function analysis at Tent Island with seal number as the grouping variable. Two views of the discriminant axes (DA) scores. (a) DA1 and DA2 (b) DA3 and DA4. Points represent individual dives, and symbols identify individual seals. Filled symbols indicate dives in which prey were recorded on the video record.

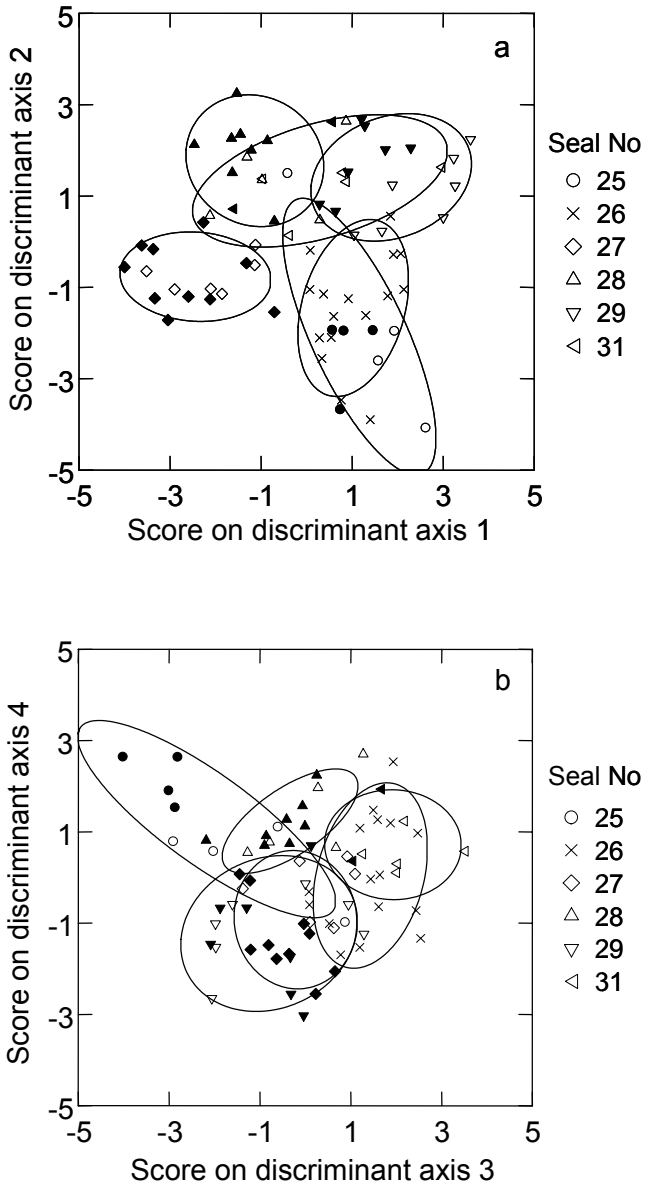
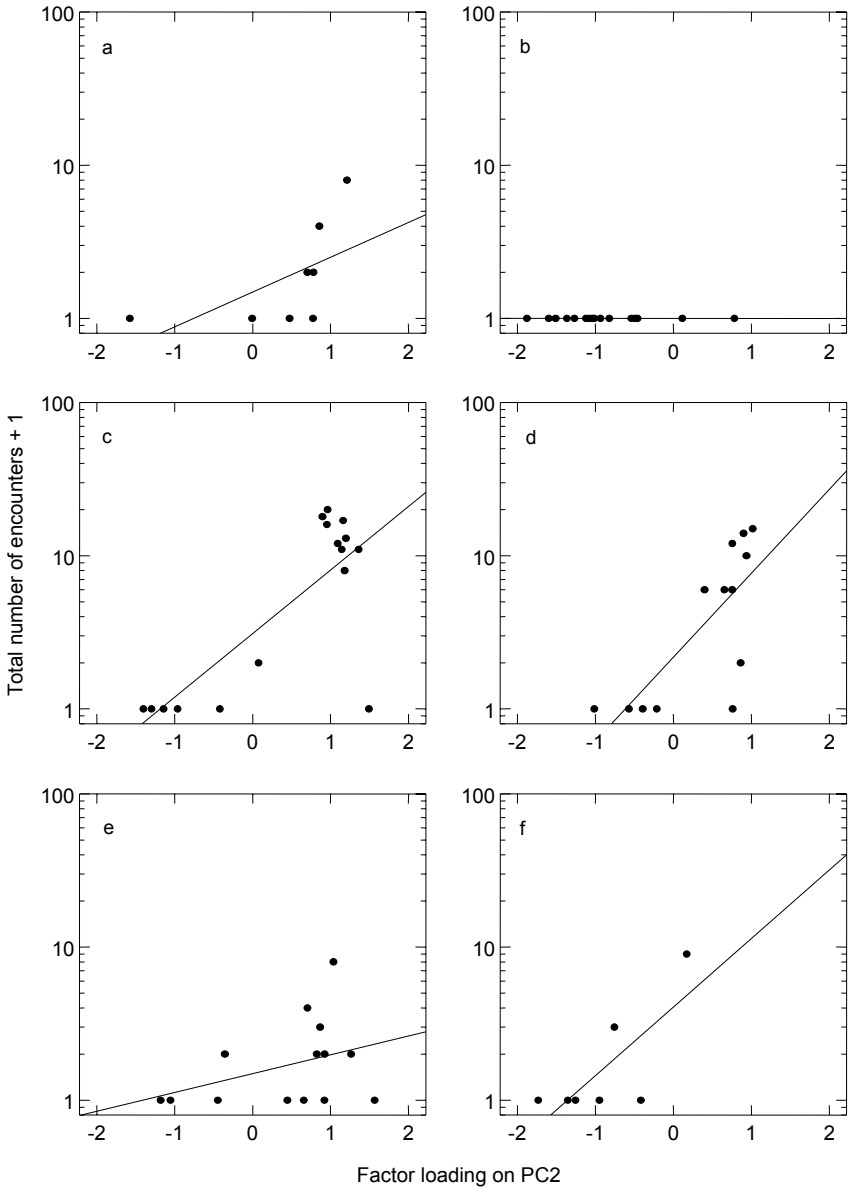


Figure 9. Relationship between total number of encounters per dive (on logarithmic scale) for Weddell seals foraging at Tent Island and score on PC2. The relationship between PC2 and foraging success was not the same for all seals, as indicated in the ANCOVA by the significant interaction between the covariate PC2 and seal number. Points represent individual dives.



Chapter 4: Structure of Weddell seal foraging dives: Comparison of free-ranging and isolated-hole seals

ABSTRACT

Weddell seals (*Leptonychotes weddellii*) foraging in the Antarctic fast-ice environment must balance their need to find food at depth with their need to replenish oxygen stores at a limited number of surface locations (breathing holes). Despite the considerable understanding of the diving behavior and physiology of Weddell seals, little is known about how foraging behavior changes when access to oxygen at the surface varies. This study compared foraging behavior of Weddell seals at a single, isolated-breathing hole with that of seals diving at locations where access to the surface was available at multiple locations (i.e., free-ranging). Comparisons were made of dive structure, hunting tactics, and allocation of time, locomotor activity, and energy based on three-dimensional dive profiles and video imagery of prey encounters for two free-ranging seals and six seals diving at an isolated-hole. Foraging dives of free-ranging seals were largely similar to those of seals diving at an isolated hole. Differences occurred in the characteristics of descent behaviors and the frequency of certain behavioral transitions. These differences appear to be responses by the seals to a greater abundance of midwater prey (*Pleuragramma antarcticum*) in the locations where free-ranging seals were diving, rather than responses by the seals to differences in breathing hole availability. Highly consistent hunting behaviors in both locations led to a predictive model for estimating foraging success from time-depth profiles. This study shows that access to multiple breathing holes does not substantially alter the foraging behavior of Weddell seals, and it provides an indication of how foraging behavior varies with prey abundance.

INTRODUCTION

Air-breathing aquatic animals must balance their need to acquire food at depth with their need to replenish oxygen stores at the surface (Kramer, 1988; Mori, 1999). To maximize the time available for foraging in the water column, these predators have increased the amount of oxygen that can be stored in their tissues and have reduced the cost of diving (Kooyman, 1989). For air-breathing predators foraging in the fast-ice environment of Antarctica, this balance is further complicated by the fact that access to oxygen while diving is restricted. Predators must locate holes in the ice in order to breathe, making breathing holes a valuable resource (Kooyman, 1981).

Weddell seals (*Leptonychotes weddellii*) are circumpolar in Antarctica and are well adapted for living and breeding in the fast-ice environment (Kooyman, 1968, 1981; Castellini et al., 1992). These seals are typically located near major perennial cracks or shoreline cracks created by tidal and wind forces. They maintain access to the surface throughout the year by using their specially adapted canines and incisors to ream the ice (Kooyman, 1981), and in locations where ice is only centimeters thick seals can break through the ice and create new breathing holes (Castellini et al., 1992). Aggressive interactions between Weddell seals are often observed in locations where seals are forced to share breathing holes. Cuts and gashes on the chest, axillary and genital regions, and flippers are commonly seen and emphasize the importance of this resource (Kooyman, 1968). During the breeding season, adult males defend underwater territories around breathing holes against other males (Castellini et al., 1992; Harcourt et al., 1998). Territories can change in size over the course of the breeding season and displacements often occur after repeated challenges. Males may share breathing holes but the volume of individual male territories can vary five-fold (Harcourt et al., 1998).

Weddell seals are capable of diving to extreme depths and traveling great distances (e.g., Kooyman, 1981; Castellini et al., 1992; Davis et al., 2003). In the fast-ice environment where breathing locations are limited, this requires that animals have well-developed sub-ice navigational abilities in order to return to breathing holes and avoid the potential of drowning (Kooyman, 1968).

The superior diving abilities of Weddell seals, combined with their hole-breathing behavior, makes them the only air-breathing predator in Antarctica that is capable of foraging in both the pelagic and benthic habitats of the ice-covered waters of the Antarctic continental shelf (Lake et al., 2003). In McMurdo Sound, the diet of Weddell seals primarily consists of small nototheniid fishes, such as Antarctic silverfish (*Pleuragramma antarcticum*) and *Trematomus* spp. However, other types of food are available, and the seals are known to feed occasionally on Antarctic toothfish (*Dissostichus mawsoni*), bald notothen (*Pagothenia borchgrevinki*), icefishes, mysids, decapod and amphipod crustaceans, octopus, and squid (e.g., Castellini et al., 1992; Burns et al., 1998; Davis et al., 1999; Fuiman et al., 2007).

Researchers have frequently taken advantage of the hole-breathing behavior of Weddell seals to study their physiology and behavior. Kooyman (1965) developed the isolated-hole protocol as a way of studying the physiology and behavior of freely diving mammals and birds in the Antarctic fast-ice environment. This technique allowed animals to dive untethered while enabling researchers to recover attached instruments and gather data. In the isolated-hole protocol, the animal is forced to return to the same location by creating a man-made hole in the ice, the location of which is chosen based on proximity to other natural holes and assumptions about the animal's diving capability. Studies at isolated-holes have provided important new insights into the physiology and ecology of Weddell seals (e.g., Kooyman et al., 1980; Qvist et al., 1986; Burns and

Castellini, 1996; Davis et al., 1999, 2003; Williams et al., 2000, 2004; Fuiman et al., 2007). By its design, however, the isolated-hole protocol restricts animals to a single breathing hole, and when only one animal is used, it prevents interactions with other seals. Therefore, the restriction of returning to a single breathing hole could alter diving behavior. For example, seals diving from an isolated-hole may be less likely to approach the physiological limits of their breath-holding ability while foraging. This could result in shorter dives in which seals spend less time at depths where prey are located, travel faster to foraging depths, or reduce the amount of stroking (and energy) needed to reach foraging depths.

The current study used the same video data recorder (VDR) deployed by Davis et al. (1999) at an isolated-hole in McMurdo Sound, but attached it to free-ranging Weddell seals instead. The free-ranging seals were released near the western shore of Tent Island, where seals naturally congregate annually. Two seals chose to move to an offshore location over deep water, an environment very much like that of the isolated-hole study. This gave us the opportunity to compare foraging behavior when seals dive in areas of similar bathymetry but have different numbers of available breathing holes. We compared dive structure, hunting tactics, and allocation of time, locomotor activity, and energy based on three-dimensional dive profiles and video imagery of prey encounters. Results showed that foraging dives did not vary substantially with differences in availability of breathing holes. Differences were found in some characteristics of descent behaviors and the frequency of certain behavioral transitions, but the majority of these differences appeared to be responses by the seals to a greater abundance of midwater prey in locations where seals had access to multiple breathing holes.

METHODS

In a previous analysis, five types of dives were identified for free-ranging Weddell seals, three of which were classified as foraging dives (Chapter 2). Group 1 dives were deep and exceeded the calculated aerobic dive limit, Group 4 dives were also deep but remained aerobic, and Group 5 dives were shallow and less than the aerobic dive limit. Deep-aerobic foraging dives (Group 4) were common at offshore breathing holes and were similar in depth and duration to the foraging dives identified by Davis et al. (2003) at an isolated-hole (Chapter 2), but in order to determine whether the isolated-hole protocol affects the structure of foraging dives, we compared the behavioral states of deep-aerobic foraging dives of the two seals diving offshore with data from a previous analysis of Weddell seals diving at an isolated-hole (Fuiman et al., 2007).

Animal capture and instrumentation

Seven adult, female Weddell seals (body mass = 463.2 ± 51.6 Kg [mean ± SD]; standard length = 241.8 ± 7.9 cm) were captured near Ross Island (77º 41' 43.4" S, 166º 20' 4.3" E), McMurdo Sound, Antarctica from October to November in 2002. Two of the seven seals (body mass = 409.7 ± 26.4 Kg; standard length = 238.8 ± 10.3 cm) moved away from the coast and dove at offshore breathing holes (Figure 11) and were used for the free-ranging dataset. The offshore breathing holes of Seals 25 and 26 represented similar foraging conditions (i.e., located away from the coastline in an area where the water column was more than 500 m deep) that were similar to the conditions of the seals diving at the isolated-hole (Figure 11). In the isolated-hole study, 10 adult seals (9 males, 1 female; body mass = 379 ± 36.3 Kg; standard length = 239 ± 9.6 cm) dove at two locations that were less than 15 km from the free-ranging dive locations (1998: 77º 51' 51.7" S, 166º 14' 26.0" E; 1999: 77º 51' 51.7" S, 166º 14' 26.0" E).

Capture and instrumentation methods were fully described by Davis et al. (1999). Briefly, seals were captured on the sea ice using a purse-string net and were transported to a field camp using a specially designed sled. Upon arrival at the field camp, animals were sedated (using ketamine and diazepam), weighed, and measured. After cleaning the fur with acetone, a piece of thin neoprene rubber was glued to the seal's back using contact cement. The neoprene rubber provided a secure but flexible attachment for the VDR. The main housing of the VDR was placed in a molded, non-compressible foam cradle and secured to the neoprene rubber with a hose clamp, Velcro, and plastic cable ties. The buoyancy of the foam cradle offset the weight of the instruments so the unit was neutrally buoyant in water. The video camera (mounted on the head), compass housing (placed behind the main housing) and accelerometer (located near the base of the tail) were glued to the fur using the same method. Free-ranging seals also had a satellite transmitter and two VHF radio transmitters glued to the fur to allow the seals to be relocated after they were released. Each animal was allowed to recover from anesthesia for approximately 18 h before it was released into a 1.3-meter diameter man-made breathing hole at the field camp.

Instruments were typically deployed for 3-5 days before the free-ranging seals were relocated and had their instruments exchanged for additional deployments (ranging from 1-6 deployments per free-ranging seal). When the seals hauled out on the ice, the satellite transmitters provided the seal's location to within a 0.5-km radius, and VHF radio transmitters allowed final localization of the seal using a receiver and directional antenna. All animals were handled in accordance with animal use protocols of The University of Texas at Austin and Texas A&M University.

Equipment

The self-contained video camera and data logger were designed to record the behavior, swimming performance, three-dimensional movements, and environment immediately in front of diving animals, and were described by Davis et al. (1999). To summarize, the data logger was contained in a torpedo-shaped, aluminum housing and recorded data from several instruments: (1) a low-light sensitive, monochrome video camera, surrounded by an array of near-infrared light-emitting diodes and located on the animal's head, (2) a pressure transducer, (3) a water speed sensor (paddle wheel), (4) a gimbaled flux-gate compass, and (5) a 1-axis accelerometer placed on the dorsal surface near the base of the seal's tail to record flipper stroking. Pressure, speed, and bearing were sampled once per second, the accelerometer was sampled 16 times per second, and the camera recorded at a rate of 30 frames per second. The light-emitting diodes enabled the camera to record images underwater in complete darkness up to a distance of ca. 1 m and further when additional ambient light was available. The infrared light source (λ_{max} = 850 nm) was assumed to be invisible to the seals and their prey (Lavigne et al., 1977). The pressure transducer was calibrated in the laboratory for water depth. The compass was calibrated at the deployment site using the position of the sun together with GPS location, time, and a navigation computer. The speed sensor was calibrated after each deployment using the method of Blackwell et al. (1999). Although it is difficult to determine with certainty the effect of the equipment on the behavior of the animal, the additional hydrodynamic drag created by the VDR did not result in significant differences in the recovery oxygen consumption for seals diving with and without the equipment (Williams et al., 2004). The frontal area of the video camera and data logger occupied < 5.5% of the frontal area of the seal. Also, the seals continued to feed successfully while

carrying the equipment, which suggests that the instrumentation did not have a large effect on foraging behavior.

Data analysis

Data and video were downloaded immediately upon recovery of the instruments. Each video tape was duplicated in VHS format and a time code was superimposed on the video display to facilitate analysis. Video tapes were reviewed for scenes of interest (e.g., encounters with prey, visible substrate, breathing hole markers) and used to build a database of observations. The two free-ranging seals encountered several types of prey offshore, including Antarctic silverfish (*Pleuragramma antarcticum*), bald notothen (*Pagothenia borchgrevinki*), and icefish (species unknown). Seals 25 and 26 performed 33 and 26 deep-aerobic foraging dives, respectively, at the offshore breathing holes (Chapter 2). Seals 25 and 26 were always successful in encountering prey when foraging in this region, so we restricted our comparison with the isolated-hole dataset (Fuiman et al., 2007) to successful foraging dives (i.e., those in which prey were encountered) of six seals (Seals 12, 14, 15, 16, 17, 18).

In the free-ranging study, locations of known breathing holes within the study area were gathered using handheld GPS units. Distinct floating markers were placed in each hole so they could be identified on the video record and matched to the handheld GPS coordinates. Seals also surfaced in unmarked breathing holes, so distinctive characteristics of the sea-ice were used to identify and name as many additional breathing holes as possible. The exact geographic location of these holes was unknown, but additional information was noted from the video record (e.g., continental slope of Tent Island, the Erebus Ice Tongue) and used to place the dives from unmarked, but named, holes in a general geographic context. If a dive began or ended at an unidentified breathing hole it could not be rendered in three-dimensions and therefore was excluded

from the analysis. Three-dimensional paths of 46 offshore free-ranging foraging dives were reconstructed for Seal 25 (n = 30) and Seal 26 (n = 16). Dive paths were computed from raw data for depth, compass bearing, and speed using traditional methods of dead-reckoning (Davis et al., 1999). The isolated-hole dataset of Fuiman et al. (2007) included three-dimensional dive paths of 61 successful foraging dives (ranging from 1 to 20 per seal; Table 15).

Identification of behavioral states and events

The structure of individual foraging dives was determined by identifying distinctive behavioral states and events using the method and catalog of behaviors developed by Fuiman et al. (2007). Names of all behavioral states and events are italicized throughout this report to avoid confusion with general descriptive terms. Transitions (i.e., changes in behavior or events) were identified by carefully examining three-dimensional dive profiles for changes in swimming path geometry, swimming speed, and stroking activity. Events were observed from the video record and included: 1) submergence of the seal's head at the beginning of a dive, 2) emergence of the seal's head at the end of a dive, and 3) encounters with prey. One type of prey not observed in the isolated-hole study of Fuiman et al. (2007) was observed in the offshore dives of this study. This added a new behavioral event, *icefish encounter*, to the behavioral catalog of Fuiman et al. (2007). *Icefish encounter* occurred whenever an icefish (species unknown) was visible on the video record and was located a few centimeters from the seal's muzzle. Behavioral states or events were assigned to the entire duration of a dive, except when an instrument failed to record data. This only occurred in a single dive when the speed sensor malfunctioned for 43 seconds. These missing data were assigned to the category *unknown*. Since the failure only occurred once, this category was not included in the behavioral catalog or the analysis of dive structure.

Sequence of behavioral events

The structure of foraging dives was depicted by an ethogram which summarized the time-activity budget of free-ranging seals foraging at offshore breathing holes. Ethograms were constructed using the method of Fuiman et al. (2007). Activity was measured by calculating the average amount of time during a dive spent in each state and was further refined by summarizing the proportion of time within a state spent stroking and gliding (gliding was defined as three or more consecutive seconds without stroking). All two-state transitions (dyads) were identified and their frequencies summed for all foraging dives of the two seals foraging offshore. Only statistically significant two-state transitions (those that occurred at a frequency greater than expected by chance) that were identified with first-order Markov chain analysis (Fagen and Young, 1979; Lehner, 1996) were included in the ethogram, unless otherwise indicated.

One behavioral state (*unknown*) and three behavioral events (*icefish encounter*, *notothen encounter*, *inter-prey interval*) did not meet the requirements of the statistical analysis (expected frequency greater than 1; Lehner, 1996) and were eliminated from the ethogram. The number of dyads observed in the offshore foraging dives (n = 2405) exceeded five times the square of the number of states and events, and was therefore sufficient for rigorous statistical analysis (Fagen and Young, 1979; Lehner, 1996). Since the seals typically encountered multiple silverfish within a dive, we also examined the multi-state transitions leading to the first *silverfish encounter* in a dive. This is a useful tool for understanding the tactics seals use to search for food in the absence of information about the location of patches of prey (Fuiman et al., 2007). In order to determine the dominant hunting sequence preceding *silverfish encounter*, the Markov chain method was also applied to the triads and tetrads (i.e., multi-state transitions) that led to the first *silverfish encounter* in the offshore foraging dives.

Isolated-hole vs free-ranging comparison

Hierarchical cluster analysis (single linkage, Euclidean distance) was used to explore patterns of similarity in diving behavior among seven seals (two free-ranging and five isolated-hole). A separate cluster analysis was performed for each behavioral state and was based on 16 descriptors (listed in Table 16) of each state. All descriptor values were the mean for each seal. Energetic cost was calculated for each behavioral state from the equation provided by Williams et al. (2004) for non-feeding Weddell seals. This equation estimates oxygen consumption during a dive from the seal's body mass, duration of the state, and the number of strokes of the hind flippers during the state. This equation does not take into account the added cost associated with processing a meal (i.e., heat increment of feeding), but was chosen because it provided a standard for calculating energy consumption throughout the entire course of a dive. The energy flux descriptor (mL O_2 kg^{-1} min^{-1}) was calculated by dividing the energetic cost (mL O_2 kg^{-1}) of each behavioral state by the mean amount of time (min) spent in that state. When a cluster analysis produced separate clusters for free-ranging and isolated-hole seals, stepwise discriminant function analysis was used to identify the descriptors that best distinguished the clusters. Wilks' λ was used to test for multivariate differences between the two clusters and jackknife classification results were examined as an indication of the strength of the differences. Following the multivariate comparisons, bivariate analyses (two-sample *t*-tests with a Dunn-Sidak correction for multiple comparisons) were used to compare each descriptor in order to better understand how a given behavioral state differed for free-ranging and isolated-hole foraging dives.

The frequency of two-state behavioral transitions in free-ranging and isolated-hole foraging dives was compared in order to determine how the sequence of behavioral states differed between the two studies. A combined seventy-five two-state transitions

were observed during the free-ranging and isolated-hole studies and the frequency of each transition was calculated for each dive. The mean frequency of each two-state transition was then compared between free-ranging and isolated-hole seals using Mann-Whitney U-tests with a sequential Bonferroni correction for multiple comparisons. To determine if hunting tactics differed between free-ranging and isolated-hole seals, a similar procedure was used to compare the sequence of behavioral states leading to the first *silverfish encounter* in a dive. The frequency of each multi-state (two-, three-, and four-state) transitions leading to the first *silverfish encounter* in a dive was calculated for each seal, and the mean frequency of each single-state and multi-state transition was then compared between free-ranging and isolated-hole seals using Mann-Whitney U-tests with a sequential Bonferroni correction. One isolated-hole seal (Seal 15) performed only one successful foraging dive and was therefore eliminated from the comparison of multi-state transitions.

Foraging success

Ascent was the primary behavior preceding *silverfish encounter* in both the isolated-hole and free-ranging studies (Fuiman et al., 2007; see Behavioral Sequence of Foraging Dives section in Results), indicating that this behavior could serve as useful tool for estimating foraging success of Weddell seals that feed on small, midwater prey. Time-depth profiles were constructed for a subset of 50 successful foraging dives from the isolated-hole and free-ranging studies and were used to calculate the number of *ascent* periods during the bottom phase (i.e., defined by Mitani et al. (2004) as the time from the beginning of the first ascent deeper than 50 m to the time of the end of the last descent deeper than 50 m) of the dive. The relationship between the number of silverfish encounters and the number of *ascent* periods during the bottom phase of a dive was modeled using geometric mean regression (Ricker, 1984). This model was validated by

comparing the predicted number of silverfish encounters with the observed number of silverfish encounters (determined from the video record) for a separate sample of 11 successful foraging dives using a paired *t*-test. All statistical analyses were performed with Systat statistical software (version 10.2; Systat Software Inc.).

RESULTS

Two free-ranging seals performed 51 successful foraging dives (46 of which were reconstructed in three-dimensions) at offshore breathing holes, while the data set for seals diving at an isolated-hole (Fuiman et al., 2007) included 61 successful foraging dives from six seals. Twice the number of prey were encountered in free-ranging foraging dives compared to isolated-hole dives (11.9 ± 0.9 [mean ± SE] and 5.8 ± 0.6, respectively). The primary prey item consumed during both studies was Antarctic silverfish (Fuiman et al., 2007; Chapter 2).

Three behavioral states (*bottom swimming*, *initial descent*, *spiral*) and two behavioral events (*toothfish approach* and *toothfish encounter*) described by Fuiman et al. (2007) were not observed in the offshore deep-aerobic foraging dives of free-ranging seals. The remaining six behavioral states (*descent*, *meandering descent*, *horizontal swimming*, *ascent*, *transit up*, and *final ascent*) and three events (*silverfish encounter*, *notothen encounter*, and *inter-prey interval*) were all observed in at least one of the 46 foraging dives. One additional event (*icefish encounter*) that was not described by Fuiman et al. (2007) also occurred during the current study. *Icefish encounter* was observed once in each of two foraging dives. Both of these encounters were made in midwater, one by each seal. Depth (238.2 ± 131.1 m) and time (10.1 ± 1.2 min) of the encounters was variable. Both icefish encounters were preceded by ascent and one was followed by ascent and one by horizontal swimming.

Comparison of behavioral states

Hierarchical cluster analyses revealed a distinct separation between free-ranging (Seals 25 and 26) and isolated-hole seals (Seals 12, 14, 16, 17 and 18) during periods of *descent* and *meandering descent*. There were, however, no strong separations between the free-ranging and isolated-hole animals for any of the other states or events (Figure 12). Discriminant analysis of *descent* and *meandering descent* periods found significant multivariate differences (Wilks' $\lambda > 0.115$, $P < 0.001$) between the successful foraging dives at an isolated-hole and successful offshore foraging dives of free-ranging seals. Discrimination of free-ranging and isolated-hole seals during *descent* was based on the greater mean depth and stroking rate of free-ranging seals and the earlier start (in time and depth) of *descent* (Tables 16 & 17). Free-ranging and isolated-hole seals were distinguished during *meandering descent* by the greater stroking rate and energy flux of free-ranging seals and their earlier cessation of *meandering descent* (Tables 16 & 17).

Discriminant analysis correctly classified 94% (jackknife results) of successful free-ranging and isolated-hole foraging dives for *descent* periods. There were significant differences in 11 of the 16 descriptors of *descent* between free-ranging (n = 46) and isolated-hole (n = 61) dives (Table 17). Seals in the free-ranging study began *descent* significantly shallower than seals at the isolated-hole. The seals finished *descent* at similar depths, but the ending time for *descent* periods was significantly later. This resulted in a longer overall duration of *descent* periods for free-ranging seals. The later ending time and longer duration of *descent* periods were not due to an increase in the average duration of individual *descent* periods, but rather, a significantly greater number of *descent* periods during free-ranging dives. Despite the significantly lower swimming speeds associated with *descent* periods for free-ranging seals, mean stroking rate was significantly higher. This coincided with a significantly greater number of total strokes

and a significantly lower amount of gliding (both total and percentage of time). Differences in stroking activity translated into energetic differences between the two groups; free-ranging seals expended more energy and at a higher rate during *descent* than seals at the isolated-hole.

Jackknife classification success for *meandering descent* was also high (94%). There were significant differences between free-ranging (n = 38) and isolated-hole (n = 57) dives in nine descriptors (Table 17). There were significantly fewer periods of *meandering descent* for free-ranging seals compared to isolated-hole seals, although there was no difference in the amount of time spent in this state. Instead, the average duration of each *meandering descent* period was longer for free-ranging seals. Free-ranging seals showed a significantly higher stroking rate during *meandering descent*, which resulted in five times as many total strokes and significantly less gliding (both total and percentage of time). Differences in stroking activity also translated into differences in total energy expended during *meandering descent*. Free-ranging seals expended more energy and at a significantly higher rate. Despite the increased stroking activity of free-ranging seals, they swam significantly slower than the isolated-hole seals.

Behavioral sequence of foraging dives

The ethogram for successful free-ranging foraging dives was much simpler than the ethogram for successful dives at an isolated-hole. Ten significant transitions were identified in the offshore foraging dives of free-ranging seals, while 21 transitions were significant for successful isolated-hole seals (Figure 13). However, all but one of the transitions (*silverfish encounter* → *transit up*) observed in free-ranging dives were also observed at the isolated-hole, indicating that the same overall foraging sequence was present in both. Offshore foraging dives of free-ranging seals began with *descent* or *meandering descent* (36 and 10 times respectively; represented by broken arrows in

Figure 13a to show how free-ranging seals began foraging dives). Once in either of these descent states, seals were likely to switch between the two. *Meandering descent* was followed by *descent* 98% of the time. *Descent* transitioned into *meandering descent* only 1% of the time, but this was still more often than expected by chance. Seals also transitioned from *descent* to *horizontal swimming* (40%). Once in *horizontal swimming*, the only significant transition was to *ascent* (61%), which in turn led to led to *silverfish encounter* (68%). After encountering a silverfish, the seals transitioned most often to *ascent* (77%), but sometimes to *transit up* (4%). From *transit up*, the only significant transition was to *final ascent* (78%), which lasted until the seals returned to the surface and ended the dive (Figure 13a).

Seventy-five different two-state transitions occurred during isolated-hole and free-ranging dives. The mean frequency of ten of these 75 transitions differed significantly between the two studies (Table 18). Many of the differences were directly related to a larger number of *silverfish encounters* in the dives of free-ranging seals. For example, there were significantly more transitions from *ascent*, *descent*, and *horizontal swimming* into *silverfish encounter* during free-ranging dives. There were also significantly more transitions out of *silverfish encounter* into *ascent*, *descent*, and *horizontal swimming*. Several of the significant differences were indirectly related to a greater number of prey encounters by free-ranging seals. The seals transitioned back and forth between *descent*, *horizontal swimming*, and *ascent* at a significantly higher frequency during free-ranging dives than they did at the isolated-hole. Finally, two of the significant differences were due to the absence of states (*initial descent*) and events (*icefish encounter*) during one of the studies.

First silverfish encounter

When the free-ranging seals foraged offshore, they encountered at least one silverfish in all 46 foraging dives. One of three states (*ascent*, *horizontal swimming*, or *descent*) immediately preceded the first *silverfish encounter* in a dive, but none occurred at a frequency greater than expected by chance. *Ascent* was the most frequent of the preceding states at 60%, while *descent* and *horizontal swimming* each preceded 20% of the first *silverfish encounters* (Table 19). Eight different two-state transitions preceded *silverfish encounter*, but only two were significant (Table 19). *Horizontal swimming* → *ascent* and *descent* → *ascent* each occurred in 30% of the dives. All other two-state transitions were non-significant and occurred in less than 15% of the dives. There were 13 three-state transitions preceding the first *silverfish encounter*, and two of those transitions were significant (Table 19). The transition from *descent* → *horizontal swimming* → *ascent* was present in 29% of the dives, while *meandering descent* → *descent* → *ascent* was present in 20%. The remaining three-state transitions were non-significant and occurred in less than 11% of the dives. Of the 15 four-state transitions, only one was significant (Table 19). The transition from *descent* → *meandering descent* → *descent* → *ascent* was present in 22% of the dives. The remaining four-state transitions were non-significant and occurred in less than 16% of the dives. Mann-Whitney U-tests (sequential Bonferroni corrected for multiple comparisons) showed no significant differences between free-ranging and isolated-hole seals in the mean frequency of multi-state transitions leading to the first silverfish encounter in a dive.

Foraging success

There was a significant positive relationship between the frequency of *silverfish encounters* and the number of *ascent* periods during the bottom phase of a dive ($r^2 = 0.56$, $t_{48} = 3.48$, $P = 0.001$; Figure 14a). The model was built on data from 50 dives and

validated using a second sub-sample of 11 time-depth profiles. On average, predicted values were slightly greater than observed values (mean difference = 1.4 encounters), but there was no significant difference between predicted and observed values (t_{10} = -1.01, P = 0.337; Figure 14b), suggesting that the number of *ascent* periods calculated from the bottom phase of time-depth profiles is useful for estimating foraging success of Weddell seals feeding on silverfish.

DISCUSSION

This study showed strong behavioral similarities between Weddell seals foraging at a single breathing hole and seals with access to multiple breathing holes. The diet of offshore free-ranging (Chapter 2) and isolated-hole (Fuiman et al., 2002) seals consisted almost entirely of Antarctic silverfish. In both groups, *ascent* was the most frequent behavior leading to and following *silverfish encounter*. The overall sequence of behaviors in successful free-ranging dives was similar to successful dives at an isolated-hole. Nine of the ten significant transitions in free-ranging dives were also significant in isolated-hole dives. There were also striking similarities in the hunting tactics used to locate silverfish. Searching during *meandering descent* and *descent* was followed by *horizontal swimming* and then *ascent* in 16% of free-ranging dives. At the isolated-hole, the same sequence occurred frequently and preceded a similar percentage of first encounters. This sequence was interpreted by Fuiman et al. (2007) as the seals detecting prey during the descent phases of a dive, pursuing the prey horizontally while the prey flee upward, and then ascending into attack.

The remarkably consistent behavioral patterns used by free-ranging and isolated-hole seals led to a model that predicts foraging success from data available in time-depth profiles, and this simple model could prove useful to researchers who are unable to directly observe underwater prey encounters. This relationship only applies to encounters

with small, midwater prey, so it is important that researchers continue their effort to simultaneously record information about feeding rate and behavior for other prey types.

Despite the remarkable consistency in foraging behavior by free-ranging and isolated-hole seals, there were a few important differences. Specifically, there were differences in the characteristics of *descent* and *meandering descent* and in the frequency of several two-state transitions. Most of the differences in *descent* and *meandering descent* were related to stroking activity. Free-ranging seals spent less than 7% of the time gliding in *meandering descent* and *descent*, while seals at the isolated-hole glided over 50% of the time in these states. Differences in stroking activity translated into significant differences in both the rate of energy expenditure and the total amount of energy expended during the descent states. For example, the energetic cost of *descent* for free-ranging seals was twice that of isolated-hole animals. In addition to the energetic savings attributed to gliding (Williams et al., 2000), Fuiman et al. (2007) surmised that gliding during *descent* and *meandering descent* would also reduce the amount of self-generated noise, thereby increasing the seal's ability to perceive prey.

Despite the benefits of gliding, free-ranging seals consistently used a smaller amount of gliding during descent behaviors than the seals that foraged at the isolated hole. An alternate explanation for this difference, other than breathing hole availability, may be related to prey availability. The free-ranging seals encountered twice as many prey per dive as the seals at the isolated-hole. The greater number of prey encounters during free-ranging dives was reflected in the frequency of two-state transitions. Transitions that involved prey, either directly or indirectly, were significantly more frequent in dives by free-ranging seals. If prey are more abundant, as appeared to be the case at the free-ranging breathing holes, gliding in order to save energy and detect prey could be less important. It may be that seals conserve more energy and are more

attentive while searching (i.e., glide more) when prey density is low or there is greater uncertainty about prey abundance, as was the case at the isolated-hole. Differences in the frequency of *meandering descent* periods may also indicate a response by seals to variations in prey abundance. Free-ranging seals used significantly fewer periods of *meandering descent* within a dive. Fuiman et al. (2007) suggested that the lateral excursions characteristic of *meandering descent* would increase a seal's chances of sensing signals from prey by widening the search path. If prey abundance was lower, the chances of isolated-hole seals locating prey may have improved by using *meandering descent* more frequently.

Prey availability also may have resulted in slight differences in the hunting tactics used to locate small, midwater prey. Free-ranging seals searched for the first silverfish in a dive by alternating between *descent* and *meandering descent* before finally transitioning into *ascent* and *silverfish encounter*. Unlike the dominant sequence at the isolated-hole, this sequence lacked a period of *horizontal swimming*. Fuiman et al. (2007) suggested that if prey are close to the seal at the time they are detected, a *horizontal swimming* period of prey pursuit may be unnecessary and could explain why the free-ranging seals transitioned directly from *descent* to *ascent*. When prey were more abundant, seals may have been closer to the silverfish when they were detected, which could explain the absence of a *horizontal swimming* period.

Previous observations from the video record have shown that silverfish occur in loose aggregations, typically located 2-4 m from one another (Fuiman et al., 2002). As the seals forage within a patch of silverfish and ascend into encounters, they gradually become shallower. After the prey scatter or are depleted (i.e., patch is no longer profitable), it is reasonable to assume that seals must descend in order to relocate the patch or to locate another patch. Transitions from *ascent* to *descent* occurred more often

in free-ranging dives, and could indicate that seals in the free-ranging study were descending after dispersing or depleting one patch of silverfish (Figure 15). This idea is also supported by the presence of more periods of *descent* at significantly later times in a dive and a lack of significant differences in the number of transitions between *meandering descent* and *descent*. This indicates that the greater number of *descent* periods are used later in free-ranging dives as the seals begin searching for a new prey patch (Figure 15).

Our results show that the structure, hunting tactics, and allocation of time, locomotor activity, and energy in foraging dives at an isolated-hole were very similar to free-ranging dives at offshore breathing holes. Differences were present between the two groups, but they do not appear to be related to differences in access to breathing holes. They are most likely a reflection of changes by the seals in response to temporal and spatial variations in prey abundance. Overall, this study reveals remarkably consistent hunting tactics in Weddell seals that do not vary significantly with differences in availability of breathing holes. Some characteristics of dives do, however, vary with the number of encounters with prey.

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Table 15. Sample size of three-dimensional foraging dives and successful foraging dives for free-ranging (FR) and isolated-hole (IH) seals.

Seal No	Study	Foraging dives	Successful foraging dives
7	IH	15	0
9	IH	6	0
10	IH	3	0
11	IH	6	0
12	IH	10	8
14	IH	25	20
15	IH	36	1
16	IH	23	18
17	IH	13	11
18	IH	3	3
25	FR	30	30
26	FR	16	16

Table 16. Standardized canonical coefficients for descriptors included in the stepwise discriminant function analysis comparing behavioral states and events of seals at an isolated-hole with free-ranging seals offshore. Coefficients in bold are those that contributed most to the discrimination of groups. Missing entries indicate variables that were eliminated from the stepwise analysis because they did not meet tolerance levels.

Descriptor	***Descent***	***Meandering descent***
Mean depth	**1.60**	0.09
Min depth	**-1.24**	-0.63
Max depth	-0.57	0.90
Mean elapsed time	-0.76	0.87
Ending time	0.33	**-1.85**
Starting time	**1.22**	0.73
Mean speed	-0.65	-0.21
Mean stroking rate	**1.32**	**2.90**
Total number of strokes	-0.52	0.75
Sum time gliding	-0.93	0.95
% time gliding	0.50	0.02
Number of periods	0.31	-0.44
Sum of time	0.70	-0.89
Duration of period	0.62	-0.37
Total energetic cost		
Energy flux		**-2.11**

Table 17. Descriptors (mean ± SE) of *descent* and *meandering descent* for free-ranging and isolated-hole foraging dives of Weddell seals. Boldface type indicates significant differences in specific traits between free-ranging and isolated-hole seals ($P < 0.05$ after Dunn-Sidak correction for multiple comparisons). Data for isolated-hole dives are from Fuiman et al. (2007).

Descriptor	***Descent***		***Meandering descent***	
	Free-ranging	**Isolated-hole**	**Free-ranging**	**Isolated-hole**
N	46	61	38	57
Mean depth (m)	219.6 ± 7.7	204.8 ± 8.7	143.8 ± 6.4	184.9 ± 7.9
Min depth (m)	**41.9 ± 12.8**	**99.5 ± 12.9**	47.8 ± 7.8	67.5 ± 8.3
Max depth (m)	330.7 ± 6.0	320.8 ± 11.7	244.3 ± 9.4	261.1 ± 12.3
Mean elapsed time (min)	4.9 ± 0.2	4.6 ± 0.2	2.7 ± 0.4	3.9 ± 0.2
Ending time (min)	**10.6 ± 0.3**	**8.3 ± 0.3**	4.1 ± 0.3	4.9 ± 0.3
Starting time (min)	1.0 ± 0.3	1.9 ± 0.2	1.3 ± 0.4	1.5 ± 0.2
Mean speed ($m\ s^{-1}$)	**1.62 ± 0.04**	**2.10 ± 0.03**	**1.64 ± 0.05**	**2.20 ± 0.04**
Mean stroking rate ($strokes\ s^{-1}$)	**0.98 ± 0.02**	**0.32 ± 0.04**	**0.98 ± 0.03**	**0.15 ± 0.03**
Total number of strokes	**250.9 ± 16.4**	**54.8 ± 8.8**	**156.2 ± 12.6**	**30.6 ± 7.7**
Sum time gliding (s)	**16.1 ± 2.2**	**119.7 ± 15.4**	**8.1 ± 1.9**	**123.9 ± 10.2**
% time gliding	**6.4 ± 0.9**	**52.7 ± 4.4**	**5.1 ± 1.1**	**66.7 ± 4.8**
Number of periods	**7.4 ± 0.4**	**4.6 ± 0.3**	**1.2 ± 0.1**	**1.7 ± 0.1**
Sum of time (min)	**255.5 ± 15.1**	**192.0 ± 14.2**	164.1 ± 9.8	167.2 ± 11.7
Duration of period (s)	37.2 ± 2.3	51.3 ± 5.1	**151.7 ± 10.7**	**106.9 ± 8.4**
Total energetic cost ($ml\ O_2\ kg^{-1}$)	**19.52 ± 1.20**	**9.21 ± 0.75**	**12.33 ± 0.82**	**7.46 ± 0.73**
Energy flux ($ml\ O_2\ kg^{-1}\ min^{-1}$)	**4.57 ± 0.06**	**3.00 ± 0.09**	**4.51 ± 0.11**	**2.60 ± 0.07**

Table 18. Mean frequency (± SE) of two-state behavioral transitions that were significantly different between free-ranging (n = 46) and isolated-hole (n = 61) foraging dives of Weddell seals. Data for isolated-hole dives are from Fuiman et al. (2007). * denotes sequences that occurred more frequently than expected by chance, as determined from a Markov chain analysis.

	Transition	Free-ranging	Isolated-hole
	Ascent → *descent*	2.5 ± 0.2	1.0 ± 0.2
	Ascent → *horizontal swimming*	2.9 ± 0.2	0.9 ± 0.1
*	*Ascent* → *silverfish encounter*	12.5 ± 0.6	3.8 ± 0.5
	Descent → *silverfish encounter*	1.8 ± 0.2	0.6 ± 0.1
*	*Horizontal swimming* → *ascent*	4.7 ± 0.3	1.6 ± 0.2
	Horizontal swimming → *silverfish encounter*	1.6 ± 0.2	0.4 ± 0.1
	Icefish encounter → *ascent*	0.3 ± 0.1	0.0 ± 0.0
	Initial descent → *turn*	0.0 ± 0.0	0.3 ± 0.1
*	*Silverfish encounter* → *ascent*	11.5 ± 0.6	3.1 ± 0.4
	Silverfish encounter → *descent*	1.9 ± 0.2	0.6 ± 0.1

Table 19. Behavioral sequences leading to the initial *silverfish encounter* in a dive and their relative frequency (%) in successful foraging dives for free-ranging and isolated-hole seals. * denotes sequences that occur more frequently than by chance, as determined from Markov chain analysis. Data for isolated-hole dives are from Fuiman et al. (2007).

Behavioral sequence	**Free-ranging**	**Isolated-hole**
Ascent	60	64*
Horizontal swimming	20	15
Descent	20	13
Transit up		9
Horizontal swimming → *ascent*	30*	30*
Descent → *ascent*	30*	28*
Descent → *horizontal swimming* → *ascent*	29*	25*
Meandering descent → *descent* → *ascent*	20*	11
Descent → *meandering descent* → *descent* → *ascent*	22*	6
Meandering descent → *descent* → *horizontal swimming* → *ascent*	16	19*

Figure 11. Map of study area within McMurdo Sound with diving locations for free-ranging and isolated-hole seals indicated by dashed lines.

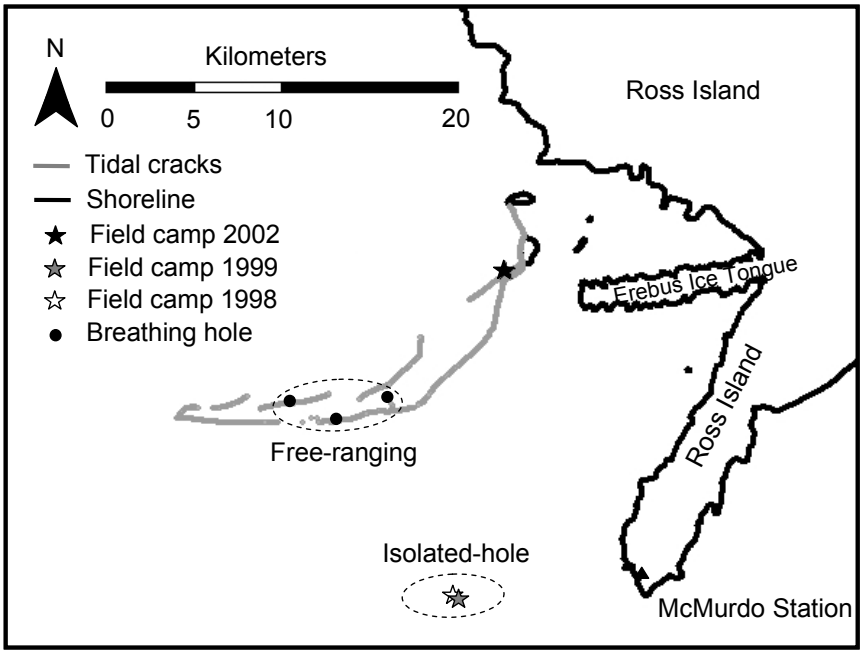


Figure 12. Results of hierarchical cluster analyses for (a) *descent*, (b) *meandering descent*, (c) *horizontal swimming*, (d) *ascent*, (e) *transit up*, (f) *final ascent*, and (g) *silverfish encounter*. Free-ranging seals (25, 26) clustered separately from seals diving at an isolated-hole (12, 14, 16, 17, 18) for *descent* and *meandering descent*.

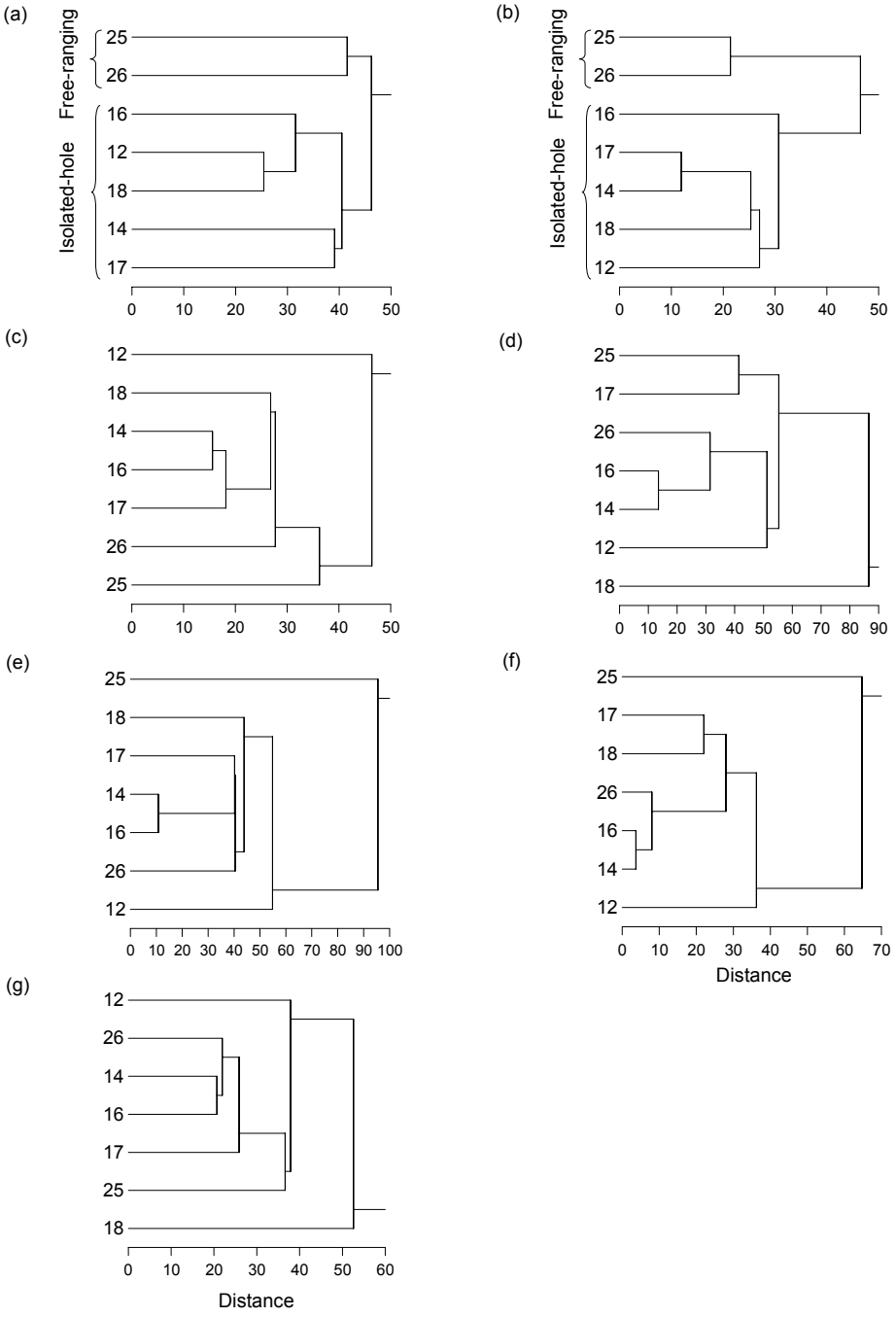


Figure 13. Ethogram depicting mean depth and elapsed time at which behavioral states and events (circles) occurred in foraging dives by (a) free-ranging (n = 46) and (b) isolated-hole seals (n = 53; adapted from Fuiman et al. [2007] Fig. 3b). Circles are scaled in proportion to the amount of time spent in each state and patterns within each circle identify the proportion of time in each state during which the hind flippers were stroking or gliding. Arrows identify transitions between states and events that occurred significantly more frequently than expected by chance. Broken arrows in (a) free-ranging ethogram show how the seals began foraging dives. Broken arrow in (b) isolated-hole ethogram shows the most frequent sequence by which seals returned to the breathing hole. Arrow widths are scaled to the proportion of all transitions from the originating state.

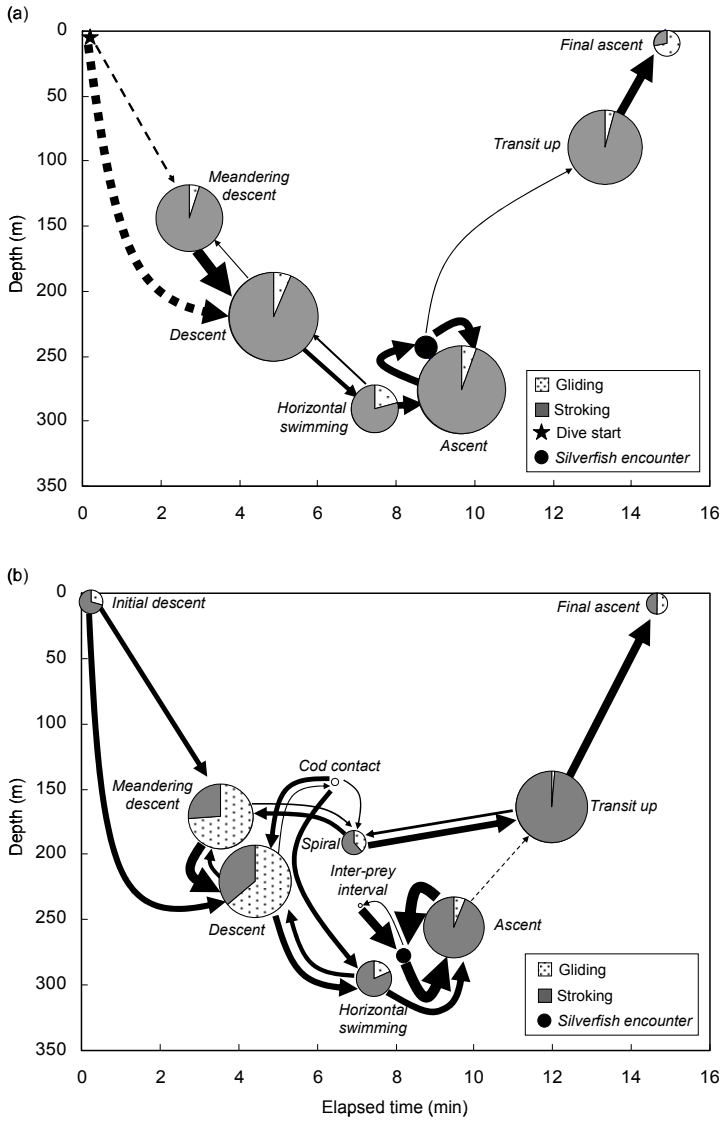


Figure 14. (a) Number of *silverfish encounters* (determined from the video record) in relation to the number of *ascent* periods during the bottom phase of dive. Regression equation: *silverfish encounters* = 1.4 + 1.7*ascents* (n = 50, r^2 = 0.56, t_{48} = 3.48, P = 0.001). (b) Relationship between predicted and observed frequency of *silverfish encounters* from the above equation based on an independent sample of 11 dives from both free-ranging and isolated-hole seals.

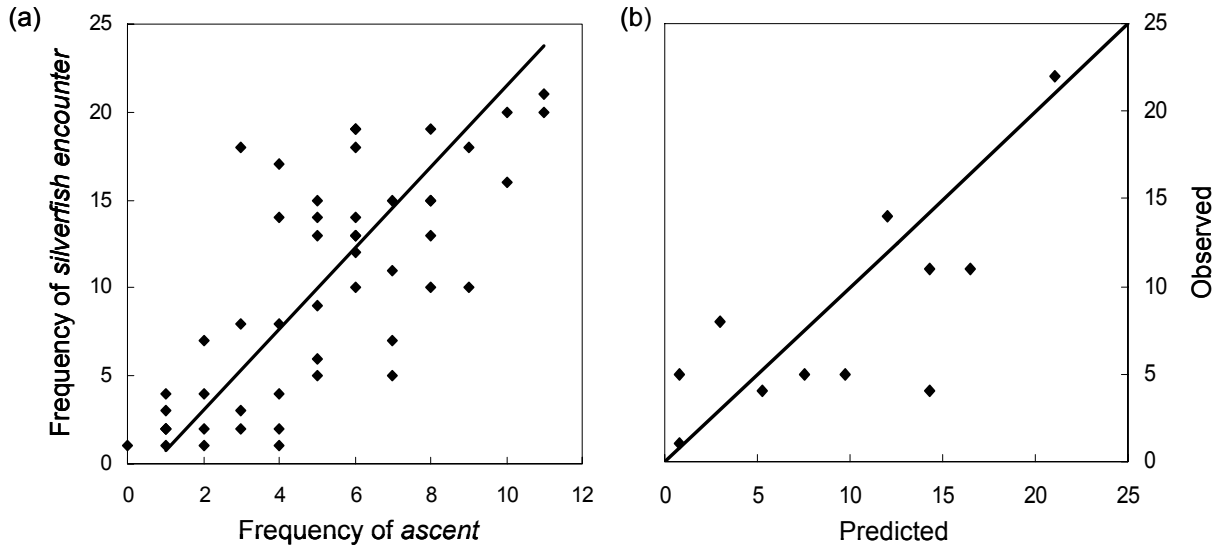
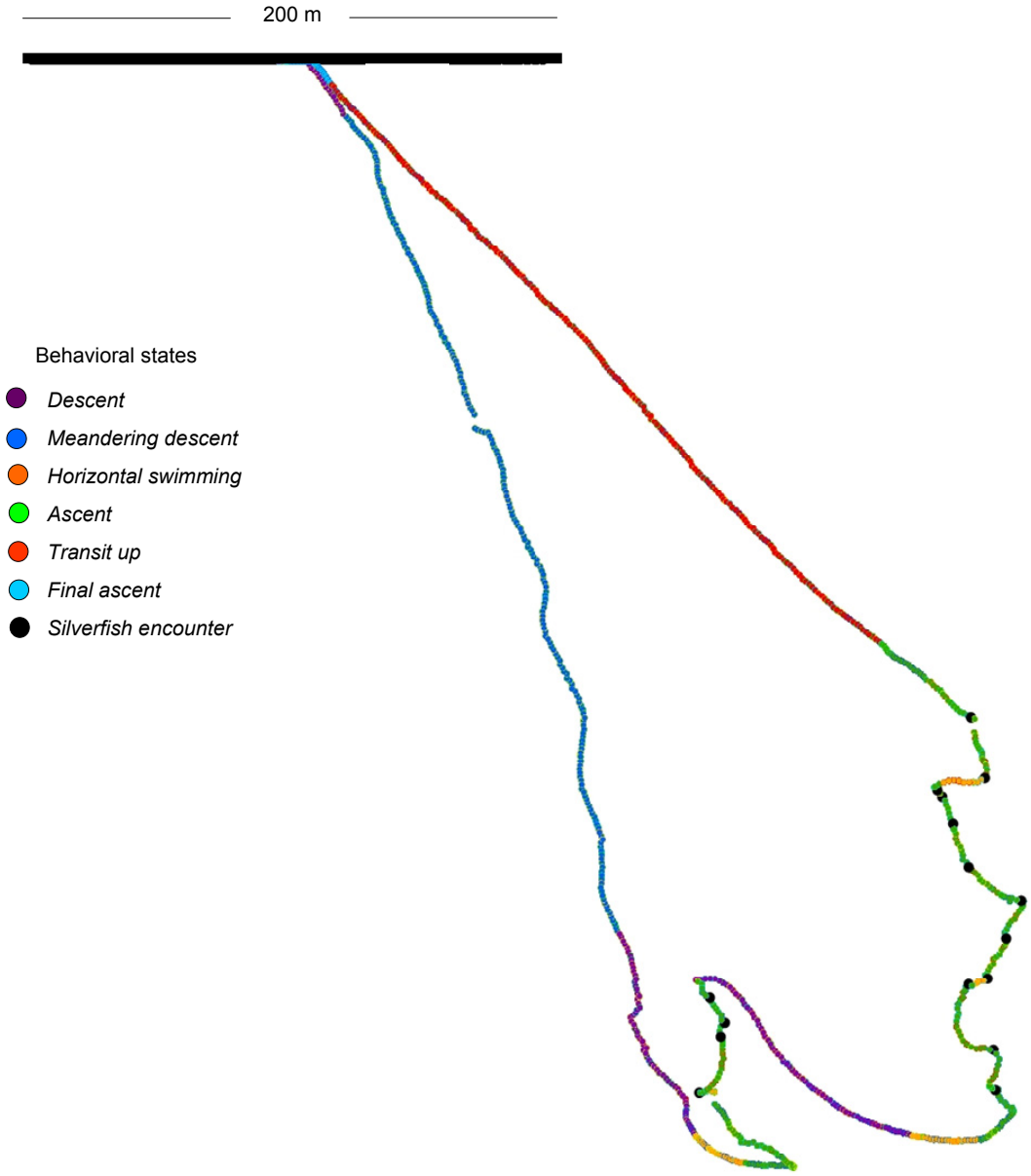


Figure 15. Three-dimensional dive profile for a representative free-ranging foraging dive at an offshore breathing hole showing different behavioral states and events. Colors represent different states. Each point represents the position, in three dimensions, of a seal at 1-s intervals during the dive. Black bar at top of figure represents both the surface of the ice and the scale of the figure in all directions.



Chapter 5: Individual variability in foraging tactics of free-ranging Weddell seals (*Leptonychotes weddellii*)

ABSTRACT

Previous studies have suggested that Weddell seals (*Leptonychotes weddellii*) foraging in McMurdo Sound, Antarctica specialize on a single prey species, Antarctic silverfish (*Pleuragramma antarcticum*), using a widely-foraging, energy-maximizing foraging tactic. The degree to which diet and foraging tactics vary among individuals has not been examined. This study examined interindividual variability in diet and foraging behavior by instrumenting seven female Weddell seals with video data recorders. Seals hunted from breathing holes at two locations: along the coastline of a small island and offshore over deep water. Diet was established using the video record and foraging behavior was interpreted from reconstructions of three-dimensional dive paths. Two seals foraging at offshore breathing holes specialized on silverfish, and differences were not found in either the time or energy spent searching or handling silverfish. . However, diet varied significantly among individuals diving from breathing holes near the coastline. Two of these coastal seals specialized on silverfish, while two others consumed both silverfish and benthic prey. This indicates that some seals have a greater diet breadth when benthic prey were more accessible along the coast. Despite increased accessibility of benthic prey in these coastal locations, silverfish, which have a high lipid concentration and occur in loose aggregations, required less handling to consume. Thus, it may be more energy-efficient for seals to specialize on silverfish at the coastal location despite the additional time and energy required to travel to the depths where silverfish are located. Our results indicate that individuals use different tactics to meet the energetic requirements of foraging in areas where the time and energy required to reach midwater

prey is great and alternate prey items are more accessible. Results also show that interindividual variability must be considered when trying to understand the basis upon which Weddell seals make foraging decisions and how these decisions may change with differences in competition, prey abundance, and prey diversity.

INTRODUCTION

Four theoretical axes have been developed to describe the foraging tactics of predators (Bell, 1990; Figure 16). Each can be viewed as a continuum that is defined by the tactics at its extremes. The first axis involves the searching behavior of the predator, where widely-foraging predators that acquire prey through extensive searching are at one extreme. Sit-and-wait predators that obtain prey by waiting in ambush, using the majority of their time for pursuit and handling of prey, are at the other. A second axis, closely related to the first, is defined by the size of prey consumed. Predators that spend considerable time searching for food usually consume relatively small prey, while animals that consume larger prey spend more time in pursuit and handling (Werner and Hall, 1974; Griffiths, 1980). The third axis is based on optimal foraging theory, which predicts that an animal will maximize its net energy gain (Schoener, 1971). Here, time-minimizers and energy-maximizers are at the extremes. Once time-minimizers have reached a certain basic energy input, they stop searching and use their remaining time for other activities. Energy-maximizers on the other hand, try to obtain as many available prey as possible, and therefore spend the most time searching for food (Bell, 1990). The fourth axis is defined by diet breadth, and the extremes include generalists that feed on any available resource and specialists that only feed on particular types of prey. The extent to which an animal is a specialist often depends on the resources available and the amount of competition for those resources. Generalists typically occur when or where

there are fewer competitors and when resource availability is higher (Glasser, 1982; Schindler et al., 1997).

For many years, researchers were unable to make observations of diet and foraging behavior of individual animals in the field (Tinker et al., 2007). As a result, individual variability in the foraging tactics of predators was largely overlooked (Bolnick et al., 2003). However, an increasing number of field studies show that individual variability in diet and foraging behavior is more common than previously thought (e.g., Heinrich, 1976; West, 1986; Werner and Sherry, 1987; Estes et al., 2003), and the potential impact of behavioral variability on spatial and temporal variation of trophic interactions is now being considered. For example, if individual dietary specialization exists within a population, the impact of any subset of the population on prey abundance may vary considerably (Tinker et al., 2007). Conversely, changes in the abundance of particular food resources could have disproportionate effects on subsets of the population. Annett and Pierotti (1999) found that individual diet was the principal factor influencing survival and reproduction in Western gulls (*Larus occidentalus*) and that individuals consuming more fish had longer breeding life spans and higher reproductive performance. Incorporation of diet and foraging behavior variability into population- and community-level models will improve the understanding of food-web dynamics (Estes et al., 2003).

Observations of the diet and foraging behavior of marine mammals have been especially difficult to make due to the inability to observe their underwater behavior. However, recent developments in bio-logging technology (i.e., the use of animal-attached instruments to study behavior) have given researchers new and powerful tools for recording the foraging tactics of individuals (e.g., Fedak et al., 2002; Kooyman, 2004; Block et al., 2005). Studies have now documented individual variability for several types

of marine mammals and birds (e.g., Boyd et al., 1991; Burns et al., 1997; Kato et al., 2000; Tremblay and Cherel, 2000; Estes et al., 2003; Austin et al., 2004; Tinker et al., 2007). Such variability has primarily been attributed to large-scale variations in prey type, abundance, or distribution that were associated with differences in foraging habitat. However, fine-scale variability within populations that exploit the same foraging habitat is more difficult to measure and has been examined much less often. Tinker et al. (2007) found that individual Southern sea otters (*Enhydra lutris nereis*) foraging in overlapping home ranges were dietary specialists that consumed one of three distinct diets. Individual dietary specialization was reflected in time-depth profiles due to differences between prey species in capture depths, relative capture frequency, and handling time. Individual variability in diet and foraging behavior may also exist in other species of diving predators that share habitats where multiple prey species are available.

Diet and foraging behavior of Weddell seals (*Leptonychotes weddellii*) have been well-described (e.g., Kooyman, 1981; Castellini et al., 1992; Davis et al., 1999, 2003; Plötz et al., 2001; Fuiman et al., 2007). These large predators are highly adapted for hunting in the cold, dark, ice-covered waters of Antarctica, and their hole-breathing behavior and superior diving abilities allow them to live under shore-fast sea ice and reach extreme depths (e.g., Kooyman, 1981; Castellini et al., 1992). They are the only air-breathing predator in Antarctica that is capable of foraging in both the pelagic and benthic habitats of the ice-covered waters of the Antarctic continental shelf (Lake et al., 2003). Weddell seal diets in McMurdo Sound were thought to vary little and have been shown to consist primarily of small nototheniid fishes such as Antarctic silverfish (*Pleuragramma antarcticum*) and *Trematomus* spp. However, other types of food are available, and the seals are known to feed occasionally on prey such as Antarctic toothfish (*Dissostichus mawsoni*), bald notothen (*Pagothenia borchgrevinki*), icefishes,

mysids, decapod and amphipod crustaceans, octopus, and squid (e.g., Castellini et al., 1992; Burns et al., 1998; Davis et al., 1999; Fuiman et al., 2007). Based on these previous accounts of diet, Weddell seals are specialists that spend large amounts of time searching and consuming large numbers of small, midwater fishes from a depauperate fauna. Thus, they appear to employ a widely-foraging, energy-maximizing strategy while diving in McMurdo Sound. The amount of individual variability in both diet and foraging behavior is unknown.

Using a video data recorder (VDR) attached to adult, female Weddell seals, we found that diet varied among individuals when seals dove in a coastal area of shallow bathymetry but not when they hunted from offshore breathing holes. Some seals had a greater diet breadth when benthic prey were more accessible, while other seals specialized on silverfish.

METHODS

Animal Capture and Instrumentation

Six adult, female Weddell seals (body mass = 463.5 ± 56.5 Kg; standard length = 242.0 ± 8.6 cm; Table 20) were captured near Ross Island (77º 41' 43.4" S, 166º 20' 4.3" E; Figure 17), McMurdo Sound, Antarctica from October to November in 2002. Capture and instrumentation methods were fully described by Davis et al. (1999). Briefly, seals were captured on the sea ice using a purse-string net and were transported to a field camp using a specially designed sled. Upon arrival at the field camp, animals were sedated (using ketamine and diazepam), weighed, and measured. After cleaning the fur with acetone, a piece of thin neoprene rubber was glued to the seal's back using contact cement. The neoprene rubber provided a secure but flexible attachment for the VDR. The main housing of the VDR was placed in a molded, non-compressible foam cradle

and secured to the neoprene rubber with a hose clamp, Velcro, and plastic cable ties. The foam cradle offset the weight of the instruments so the unit was neutrally buoyant in water. The video camera (mounted on the head), compass housing (placed behind the main housing) and accelerometer (located near the base of the tail) were glued to the fur using the same method. A satellite transmitter and two VHF radio transmitters were also glued to the fur to enable us to relocate the seals once they were released. Each animal was allowed to recover from anesthesia for approximately 18 h before it was released into a 1.3-meter diameter man-made breathing hole at the field camp.

Instruments were typically deployed for 3-5 days before the free-ranging seals were relocated and had their instruments exchanged for additional deployments (ranging from 1-6 deployments per seal). When the seals hauled out on the ice, the satellite transmitters provided the seal's location to within a 0.5-km radius, and VHF radio transmitters allowed final localization of the seal using a receiver and directional antenna. All animals were handled in accordance with animal use protocols of The University of Texas at Austin and Texas A&M University.

Equipment

The VDR was designed to record the behavior, swimming performance, three-dimensional movements, and environment immediately in front of diving animals, and was fully described by Davis et al. (1999). To summarize, the data logger was placed inside a torpedo-shaped, aluminum housing and placed in a non-compressible foam cradle on the animal's back. The data logger recorded data from several instruments: 1) a low-light sensitive black and white video camera, located on the animal's head and surrounded by an array of infrared light-emitting diodes, 2) a pressure transducer, 3) a water speed sensor (paddle wheel), 4) a gimbaled flux-gate compass, and 5) a small 1-axis accelerometer placed on the dorsal surface near the seal's tail. The transducers for

pressure, speed, and bearing were sampled once per second, the accelerometer was sampled 16 times per second, and the video camera recorded at a rate of 30 frames per second. Light-emitting diodes enabled the camera to record images underwater at depths where ambient light prevented video recording. When additional ambient light was available, objects were visible at much greater distances. The infrared light source (λ_{max} = 850 nm) was believed to be invisible to the seals and their prey (Lavigne et al., 1977), which prevented any alterations in normal behavior due to the presence of artificial light. The pressure transducer was calibrated in the laboratory for water depth and the compass was calibrated at the deployment site using the position of the sun together with GPS location, time, and a navigation computer. The speed sensor was calibrated after each deployment using the method of Blackwell et al. (1999). Although it is difficult to determine with certainty the effect of the equipment on the behavior of the animal, the additional hydrodynamic drag created by the VDR did not result in significant differences in the recovery oxygen consumption for seals diving with and without the equipment (Williams et al., 2004). Also, the frontal area of the video camera and data logger occupied < 5.5% of the frontal area of the seal. The seals continued to feed successfully while carrying the equipment, which suggests that the instrumentation did not have a large effect on foraging behavior.

Data Analysis

Data and video were downloaded immediately upon recovery of the instruments. Each video tape was duplicated in VHS format and a time code was superimposed on the video display to facilitate later analysis. The video tapes were reviewed for scenes of interest (e.g., encounters with prey, substrate visible, breathing hole markers) and used to build a database of observations. Interactions with several types of prey were documented, including encounters with silverfish, *Trematomus* spp., bald notothen,

icefish (species unknown), squid, octopus, krill, and several unidentifiable prey items. Video and data were gathered for 200 dives (9 to 60 dives per seal) throughout the study, but only 135 of those dives (7 to 51 dives per seal) were identified as foraging dives (Chapter 2). Of the 135 foraging dives, only 76 could be rendered in three-dimensions. These 76 dives were made by four seals (Seals 25, 26, 27, 28) and ranged in number from 7 to 44 per seal (Table 20). Dive paths were computed from raw data for depth, compass bearing, and speed using traditional methods of dead-reckoning as described by Davis et al. (1999).

Locations of breathing holes within the study area were gathered using handheld GPS units, and distinctive floating markers were placed in each hole so they could be identified on the video record and matched to the handheld GPS (global positioning system) coordinates. When the seals surfaced in unmarked breathing holes, distinctive underwater characteristics of the sea ice were used to identify as many individual breathing holes as possible. The geographic location of these holes was unknown, but additional information was noted from the video record (e.g., continental slope of Tent Island, the Erebus Ice Tongue) and used to place the dives from unmarked, but identified, holes in a general geographic context. If the breathing hole could not be identified (either from hole markers or under-ice features), the dive could not be rendered in three-dimensions. However, these dives were included in the diet analysis since the video record was available. The seals foraged in two small areas within McMurdo Sound (Figure 17). All six seals dove at breathing holes along the western coastline of Tent Island, and two of the six seals (Seals 25 and 26) traveled away from the coastline and also dove at offshore breathing holes located over deeper water (ca. 500 m). These locations were examined separately and we assumed that prey were available at each location throughout the 2-month study period.

Identification of diet and foraging states

Diet was determined by recording the type and number of prey present on the video record for 91 successful foraging dives (2 to 46 per seal; Table 20). Prey captures (i.e., ingestion of prey documented on video record) and encounters (i.e., prey seen on the video record but not ingested) were recorded separately, and only those items that were ingested were included in the diet. Antarctic silverfish dominate the midwater fish fauna in this region of Antarctica (La Mesa et al., 2004) and previous studies have reported that the diet of Weddell seals in McMurdo Sound primarily consists of these small, midwater, schooling fish (e.g., Castellini et al., 1992; Burns et al., 1998; Fuiman et al., 2002). Due to the dominance of silverfish in the diet within this region, prey captures were classified into two groups: *silverfish capture* and *other capture.* The proportion of silverfish in the diet (i.e., number of *silverfish captures* divided by total number of captures) was calculated for each dive.

The video record and 3D dive paths were used to divide foraging dives into the traditional components of the foraging cycle (i.e., foraging states): search, pursuit, attack, and handling. Searching was the process of finding a food resource, pursuit and attack involved the chasing and stalking of prey, and handling included subduing and swallowing the food (Curio, 1976; Bell, 1990). After careful examination of 3D dive paths and the associated data (swimming speed, flipper stroking rate, video record), foraging states were identified and assigned to each foraging dive (Table 21, Figure 18). This partly subjective approach to identifying behavioral states has a long tradition in behavioral research (Fagen and Young, 1979) and takes advantage of the investigator's experience and biological intuition. It also allows for simultaneous integration of spatial, temporal, and behavioral information. Transitions between states (changes in behavior) were used to delimit foraging states and were recognized by changes in dive path

geometry, speed, and stroking activity as viewed by rendering each 3D dive profile with computer software that allowed rotation of the reconstructed dive in all directions (ArcScene, a component of ArcInfo 8.3, ESRI). Speed and tail stroking were color coded separately. Foraging states were operationally defined by the changes in behavior (i.e., swimming path, speed, stroking activity, ingestions of prey, and/or head movements) that marked the onset and offset of a state (Table 21). The time and energy spent in each foraging state was summed for each dive and then divided by the dive duration to determine the percentage of time and energy spent in each foraging state per dive. Energetic cost was calculated for each behavioral state from the equation provided by Williams et al. (2004) for non-feeding Weddell seals. This equation estimates oxygen consumption (mL O_2 kg^{-1}) during a dive from the seal's body mass, duration of the foraging state, and the number of strokes of the hind flippers during the state. This equation does not take into account the added cost associated with processing a meal (i.e., heat increment of feeding), but provided a standard method for calculating the energetic cost throughout the entire duration of a foraging state. Elapsed time and depth of every transition between states was recorded for each 3D dive profile. Time outside of the foraging cycle was assigned to one of three non-foraging states: *pre-foraging*, *post-foraging*, and *non-foraging* (Table 21). An additional category called *unknown* was also used when the speed sensor malfunctioned for 43 seconds during a single dive so that foraging states could be assigned to this portion of the dive.

Individual variability in foraging tactics

Foraging tactics (defined by Bell [1990] as the specific actions comprising a group of related and often sequential behaviors that, when successful, lead to the localization of food) of individuals were inferred from data on diet and foraging behavior. Seals were compared for differences in diet using the percentage of silverfish (vs. other

prey) captured in each dive. Analysis of similarity (ANOSIM) was used to compare diets of seals diving along the coastline of Tent Island because of the large number of dives in which only silverfish were encountered (i.e., 100%), which violated the assumption of normality for parametric statistical tests. ANOSIM is the non-parametric equivalent of analysis of variance test (ANOVA) and tests for differences between groups using a permutation method on a rank similarity matrix (Clarke and Warwick, 2001). Pairwise comparisons were made to determine differences among individuals. At the offshore breathing holes, Mann-Whitney U-tests were used to compare Seals 25 and 26 for differences in diet. The ANOSIM was conducted using Primer statistical software (version 6.0, Plymouth Marine Laboratory), while all other analyses were conducted with Systat (version 10.2; Systat Software Inc.).

Foraging behavior of individual seals was compared using the percentage of time and energy spent in the different foraging states. The number of prey captured per dive was included as a covariate in a one-way multivariate analysis of covariance (MANCOVA) to determine the effect of foraging success and individual variability on the time spent in *search*, *pursuit*, *attack*, and *handling*. When significant effects were found, one-way ANCOVAs were used to determine which of the foraging states (s*earch*, *pursuit*, *attack*, and *handling*) were significantly different among individuals. At Tent Island, pairwise comparisons (using Bonferroni correction for multiple comparisons) were made to determine differences among individuals. The same procedure was repeated to explore the effect of individual variability and foraging success on the energetic cost of foraging states. Separate analyses were conducted for seals diving at Tent Island and offshore.

RESULTS

Seals captured prey at both locations throughout the study period. Silverfish constituted 96.1% of the diet at Tent Island and 99.5% of the diet offshore. Only a small number of *other captures* were observed at the two foraging locations (8 *other captures* at Tent Island and 4 captures offshore). Seals at both locations spent the majority of their foraging time searching for prey (84.6% at Tent Island and 67.4% offshore), and a much smaller percentage of time in pursuit (9.0 and 20.1%, respectively), attack (5.4 and 10.3%), or handling (1.0 and 2.2%). Qualitatively similar results were obtained for the energetic cost of each foraging state. Seals expended the largest proportion of their foraging energy in search (82.6 and 64.5%), and a much smaller percentage in pursuit (11.3 and 24.1%), attack (5.1 and 8.6%), and handling (1.0 and 2.8%).

Individual variability in foraging tactics

Seals differed significantly in the percentage of silverfish in their diet when foraging at Tent Island (Figure 19a; ANOSIM, $R = 0.23$, $P = 0.003$). The diet of Seal 28 consisted entirely of silverfish, and Seal 27 also consumed a very high percentage of silverfish (average ± SE: 99.3 ± 0.7). Seal 25 consumed the lowest percentage of silverfish in its diet (25.0 ± 25.0), and Seal 29 was intermediate (64.3 ± 18.0). Diets of the two seals diving offshore were not significantly different from one another (Figure 16b; Mann-Whitney test, $U = 371.5$; $P = 0.808$); both Seals 25 and 26 consumed silverfish almost exclusively (99.3 ± 0.5 and 99.6 ± 0.4, respectively). Seal 31 captured prey in only two dives and was therefore eliminated from the analysis.

For seals diving at Tent Island, there were significant differences in the relationship between the percentage of time spent in the foraging states and foraging success (number of prey caught) (MANCOVA, $F_{8,24} = 3.35$, $P = 0.01$). Closer examination showed that the differences were in *attack* (Figure 20a; ANCOVA, $F_{2,15} =$

6.44, P = 0.01) and *handling* (Figure 20c; $F_{2,15}$ = 8.23, P = 0.004), but not *search* ($F_{2,15}$ = 0.33, P = 0.725) or *pursuit* ($F_{2,15}$ = 0.27, P = 0.766). Individuals also differed in the relationship between foraging success and energy expended (MANCOVA, $F_{8,24}$ = 4.16, P = 0.003). As with the percentage of time, significant differences were in *attack* (Figure 19b; ANCOVA, $F_{2,15}$ = 6.55, P = 0.009) and *handling* (Figure 19d; $F_{2,15}$ = 10.55, P = 0.001), but not *search* ($F_{2,15}$ = 0.36, P = 0.702) or *pursuit* ($F_{2,15}$ = 0.18, P = 0.836). Individuals were also significantly different in the percentage of time (Figure 21a; ANCOVA, $F_{2,15}$ = 5.77, P = 0.014) and energy (Figure 21b; $F_{2,15}$ = 4.8, P = 0.024) spent in *pursuit*. Seal 27 spent significantly more time and energy in *pursuit* than Seals 25 and 28.

At offshore breathing holes, there was no significant multivariate difference among seals in the relationship between percentage of time spent in the foraging states and foraging success (MANCOVA, $F_{4,48}$ = 0.13, P = 0.971). There was also no significant difference between seals in the percentage of time spent in the foraging states (MANCOVA, $F_{4,48}$ = 0.12, P = 0.975), and foraging success did not have a significant effect on the time spent in foraging states (MANCOVA, $F_{4,48}$ = 1.69, P = 0.167). Similar results were obtained when the percentage of energy expended in the different foraging states was compared among seals, using foraging success as a covariate. There was no significant multivariate difference among seals in the relationship between foraging success and energy expended (MANCOVA, $F_{4,48}$ = 0.12, P = 0.973). There was also no significant difference between seals in the percentage of energy invested in the foraging states (MANCOVA, $F_{4,48}$ = 0.14, P = 0.967) and foraging success did not have a significant effect on the time spent in foraging states (MANCOVA, $F_{4,48}$ = 1.66, P = 0.174).

DISCUSSION

Weddell seals foraging in McMurdo Sound appear to be specialists that feed primarily on one species of small, aggregated, midwater prey. Previous studies also have reported that Antarctic silverfish constitute the majority of the diet of Weddell seals in McMurdo Sound (e.g., Castellini et al., 1992; Burns et al., 1998; Davis et al., 1999; Fuiman et al., 2007). The majority of the seals' foraging time (73.5%) and energy (69.9%) was spent searching for food and varied only slightly between foraging locations. Predators that spend the majority of their time searching tend to consume many small prey (Werner and Hall, 1974, Griffiths, 1980), as was found for Weddell seals. Therefore, based on average values for the entire group sampled, Weddell seals foraging in McMurdo Sound appear to fit the characterization of widely-foraging, energy-maximizing predators that specialize on small prey.

When individuals were compared, the two seals foraging offshore over deep water consumed silverfish almost exclusively and spent similar amounts of time and energy in search, pursuit, attack, and handling. Seals diving from breathing holes at Tent Island, however, displayed significant individual variability in diet breadth and foraging behavior. Along the coastline, silverfish were less important and benthic prey were more important in the diet of two of four seals. Silverfish constitute the majority, both in abundance and biomass, of pelagic fishes in McMurdo Sound, but there is also a variety of benthic prey in this region (Friedrich and Hagen, 1994; La Mesa et al., 2004). The shallow bathymetry at Tent Island forced the seals to descend at a slower rate and travel farther in the horizontal plane in order to reach the minimum depth (155 m) at which silverfish were located (Chapter 2), effectively reducing their descent rate. As the seals traveled to and from these depths, the sea floor was often visible on the video record, indicating that the seals frequently swam close to the substrate. This behavior would

increase their chances of encountering benthic prey items, compared to seals diving offshore. In fact, 75% of non-silverfish captures at Tent Island were benthic animals. In contrast, seals diving offshore approached the sea floor twice, but consumed no benthic prey, and there was no difference in the diet of these two individuals. Lake et al. (2003) found similar results for a population of Weddell seals foraging in the Vestfold Hills region. In the southern part of their study area, the seals consumed more benthic fishes and prawns, while seals in the northern region primarily fed on silverfish. Lake et al. (2003) suggested that when travel time to the benthic foraging zone is short (i.e., shallow water areas), the tendency to feed on small pelagic fishes may be lost. They believed this could account for the high ratio of benthic to pelagic fishes consumed in the shallow, southern Vestfold Hills region, rather than a lack of pelagic fishes.

In addition to being harder to reach, silverfish may also be less abundant along the coastline of Tent Island. Adult seals tend to congregate along the coast during the summer breeding season (e.g., Kooyman, 1968; Castellini et al., 1992) and Testa et al. (1985) suggested that these aggregations may reduce the local abundance of pelagic prey. When Weddell seals foraged in an area where silverfish were less abundant and competition was higher (Tent Island), some seals consumed both benthic and pelagic prey. In an area where silverfish were potentially more abundant and competition was lower (offshore), both seals consumed silverfish almost exclusively. Thus, prey abundance and intraspecific competition appear to have an effect on diet breadth. For example, Seal 25 had the broadest diet of all seals at Tent Island but consumed silverfish almost exclusively when foraging offshore. This contradicts previous studies that found greater dietary specialization when food abundance was limited and intraspecific competition was high, and wider diet breadth when food abundance was high and competition was low (Glasser, 1982; Schindler et al., 1997). Tinker et al. (2004)

suggested that individual dietary specialization in sea otters was the result of increasingly limited prey resources, and Bentall (2005) found that sea otters were not dietary specialists in a food-rich environment. It is important to consider though, that the Weddell seals in the current study had limited access to breathing holes and were strongly affected by the bathymetry of the foraging area. Seals diving from breathing holes along the coastline are forced to travel greater distances for longer periods of time and expend more energy to find and forage in patches of silverfish. In contrast to previous studies, the high energetic cost of searching for silverfish in coastal areas may explain why some seals have a wider dietary breadth when silverfish abundance is low and competition is high.

Why would some seals at Tent Island continue to consume silverfish almost exclusively when silverfish are harder to reach and possibly less abundant? Previous studies have documented elevated foraging intake rates for specialists and attributed that to more efficient searching and/or handling times (Heinrich, 1976). At Tent Island, the two seals specializing on silverfish had the greatest foraging success, while the two seals with broader diets caught fewer prey (Chapter 3). It appears that specializing on silverfish results in greater foraging success. More efficient searching strategies, however, were not the cause of the higher foraging intake rates. The amount of time spent searching per prey was not significantly different among seals. In other words, seals spent similar amounts of time and energy searching, regardless of differences in diet breadth, and differences in searching efficiency for benthic vs. midwater prey did not explain differences in foraging success.

There were, however, significant differences among individuals in handling efficiency. There was a significant positive relationship between the amount of time (and energy) spent handling prey and foraging success (number of prey caught), but the

relationship was different among seals (Figure 19). The slope of this relationship was greatest for the seal that consumed larger numbers of benthic prey. In other words, handling benthic prey (such as *Trematomus* spp. and icefishes) was more costly in terms of time and energy than handling silverfish. This could explain the differences in foraging intake rates and the tendency for some seals to specialize on silverfish at coastal breathing holes. If the amount of time and energy required to handle prey is low, specializing on silverfish may allow seals to capture more prey, and it may be advantageous in an area where the energetic cost of traveling to and from silverfish patches is high. In addition, the lipid and fatty acid composition of fishes in Antarctica is known to vary with lifestyle and could also affect the foraging tactics used at Tent Island. In Antarctica, benthic prey items have lower concentrations of lipids and fatty acids than pelagic species (Clarke, 1983; Clarke and Peck, 1991; Friedrich and Hagen, 1994). Midwater silverfish have high concentrations of lipids (Hagen et al., 2000), and although they are smaller than most benthic prey items, their high lipid concentrations may make them a better food source by providing high-energy food at a lower handling cost than benthic prey. If so, specializing on silverfish may be an energy-efficient foraging tactic at Tent Island despite the greater accessibility of alternate food resources on the sea floor.

Seals also differed in the relationship between time (and energy) spent in attack and the number of prey captured. This relationship was positive for all seals, but similar to handling time, slopes were lower for seals that specialized on silverfish. This may suggest some interesting differences in how seals hunt for benthic and midwater prey. Attack behavior was identified by a decrease in stroking rate and speed prior to prey capture (Figure 22). A decrease in stroking rate would reduce the amount of self-generated noise produced by the seal and could potentially allow the seal to be more attentive to signals from prey, whether they be visual, chemical, or mechanical (Fuiman

et al., 2007). In the case of midwater prey such as silverfish, short duration attack periods could be used to pinpoint the location of prey at close distances after periods of vigorous stroking during pursuit (Figure 22a). When hunting prey that live a low-energy, sluggish lifestyle near the sea floor (Clarke, 1984; Clarke and Peck, 1991; Friedrich and Hagen, 1994), more stalking (i.e., longer attack) may be required in order to capture prey (Figure 22b). When prey are less mobile, less chasing (i.e., shorter pursuit) would also be expected. This was true for the seal that consumed more benthic prey (Seal 25). Seal 25 spent significantly less time in pursuit than Seal 27 which consumed silverfish almost exclusively. Therefore, lifestyle of the prey (benthic vs. pelagic) appears to have an effect on the time and energy needed for pursuit and attack and may be an important factor for determining whether seals feed on benthic and/or pelagic prey at Tent Island.

Seal 28 also specialized on silverfish at Tent Island but spent significantly less time in pursuit than the other seal that foraged on silverfish (Seal 27). Why would two seals foraging on the same prey spend different amounts of time in pursuit? One possible explanation is an increased number of prey encounters. It is reasonable to assume that more chasing is required in order to capture a greater number of silverfish. However, there were no significant differences among individuals in the relationship between time and energy spent in pursuit and number of prey captured, indicating that differences in foraging success were not related to differences pursuit. Another possible explanation is differences in the distance at which seals detect prey and begin pursuit. If seals are closer to silverfish when they are detected, less time and energy may be needed to chase prey. Previous observations from the video record have shown that silverfish occur in loose aggregations, typically located 2-4 m from one another (Fuiman et al., 2002). If silverfish are more abundant and seals encounter a dense patch of silverfish, less pursuit may be needed as compared to seals foraging on multiple patches and/or more loosely

aggregated patches of silverfish. If silverfish are not as abundant, more chasing may be needed, either within or between patches, and may explain why Seal 27 spent more time in pursuit. Thus, prey density, in addition to lifestyle of the prey, may affect the hunting tactics of seals at Tent Island.

The variability observed among individuals diving at Tent Island may be related to differences in foraging motivation. Adult Weddell seals tend to congregate along coastlines for the summer breeding season (e.g., Kooyman, 1968; Castellini et al., 1992; Testa, 1994), reaching peak numbers during December (Kooyman, 1981). If mating became more important for some individuals as the study season progressed, it is possible that the motivation to forage could have changed and resulted in differences in diet and foraging tactics. Seals 27-29 were instrumented later in the season (Nov 7 – Dec 5) when the need to reproduce was stronger and seals were congregated for breeding. Seal 29 consumed less silverfish and more other types of prey than Seals 27 and 28. The generalist foraging tactic of Seal 29 resulted in a lower capture rate, and may indicate that Seal 29 was more concerned with reproduction than foraging. This would initially support the idea that differences in foraging motivation affect foraging tactics. However, Seal 25 was also a generalist, consuming more other types of prey than any other seal. Seal 25 was instrumented earlier in the season (Oct 27 – Nov 7), when reproductive motivation was probably lower. This idea was supported by the fact that Seal 25 traveled several kilometers offshore away from Tent Island in order to forage in a location where silverfish were easier to access and possibly more abundant. The generalist foraging tactic used by Seal 25 at Tent Island does not appear to be the result of a change in foraging motivation due to reproduction. Therefore, it appears that variability in foraging tactics are not due to differences in foraging motivation, but are more likely determined by inherent differences between individuals.

Because the number of seals sampled at both locations was limited, our conclusions are speculative. However, our results suggest that foraging costs vary with prey type and that diet breadth may be greater when Weddell seals forage from breathing holes along the coastline. When benthic prey were more accessible along the coastline, two seals specialized on silverfish, while two others consumed both silverfish and benthic prey. However, silverfish have a high lipid content, occur in loose aggregations, and require less handling, which may make specialization on silverfish a more energy-efficient tactic at the coastal location despite the additional time and energy required to travel to the depths where silverfish are located. Our results indicate that individuals use different tactics to meet the energetic requirements of foraging in areas where the time and energy required to reach midwater prey is great and alternate prey items are more accessible. Results also show that interindividual variability must be considered when trying to understand the basis upon which Weddell seals make foraging decisions and how these decisions may change with differences in competition and prey abundance and diversity.

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Table 20. Mass, length, and sample size of dives for six adult, female Weddell seals included in diet analysis and identification of foraging states at Tent Island and offshore breathing holes.

			Number of dives			
			Diet		Foraging states	
Seal No	Mass (Kg)	Length (cm)	Tent Island	Offshore	Tent Island	Offshore
25	391.0	231.5	4	42	5	39
26	428.4	246.0	0	18	0	16
27	459.2	232.0	10		9	
28	466.6	245.0	7		7	
29	559.8	253.5	7		0	
31	476.0	244.0	2		0	

Table 21. Operational definitions of foraging and non-foraging states exhibited by free-ranging Weddell seals during foraging dives in McMurdo Sound, Antarctica.

Foraging state	Definition
Search	Process of finding food resources; characterized by lower stroking activity (seal often switching between stroking and gliding [defined as 3 continuous seconds of no stroking]) but relatively constant swimming speeds; typically associated with descent behavior but sometimes meandering descent (alternating right and left turns during descent [Fuiman et al. 2007]) as well
Pursuit	Chasing down of food resources; characterized by an increase in stroking activity and swimming speed; often associated with a sharp change in direction
Attack	Stalking of food resources; characterized by a decrease in stroking activity and swimming speed (can be followed by small subsequent increases though)
Handling time	Processing of food resource (i.e., subduing and swallowing); determined by the presence of prey and observations of head movements of the seal and prey on the video record
Non-foraging	
Unknown	Speed sensor failed to record data
Pre-foraging	Begins when the seal departs the breathing hole and ends when the seal began searching; often associated with a change in direction, beginning of stroke and glide behaviour, and/or a switch from descent to meandering descent
Post-foraging	Onset was marked by the seals transition into transit up (linear ascent to the hole that was marked by noticeably high frequency, low amplitude lateral displacements in the path [Fuiman et al. 2007]); associated with high speeds and high frequency stroking
Non-foraging	Time when the seal exited the foraging cycle but subsequently returned to it later in a dive - typically occurs when seal is returning to the breathing hole but encounters additional prey during its ascent; onset is typically marked by the beginning of transit up and the end is associated with a change in direction and a decrease in stroking rate and speed

Figure 16. Four axes used to define the foraging tactics of a predator (Adapted from Bell, 1991).

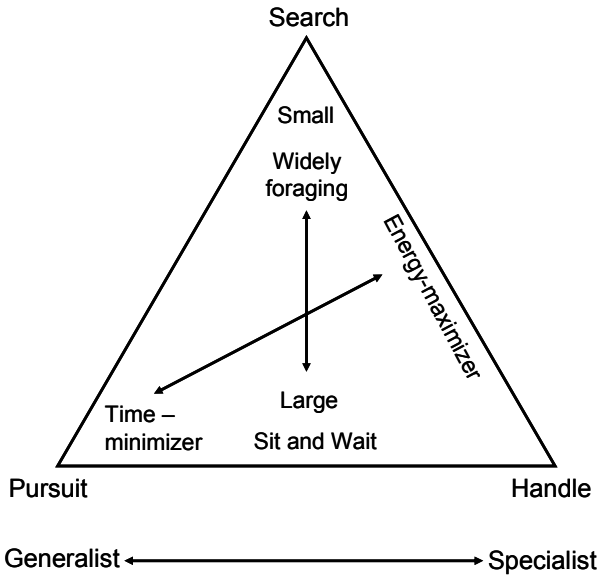


Figure 17. Map of study area within McMurdo Sound with diving locations enclosed by a dashed line. All seals dove along the west coast of Tent Island, but two seals (Seals 25 and 26) traveled away from the coastline and dove at offshore breathing holes located over the deeper waters of McMurdo Sound.

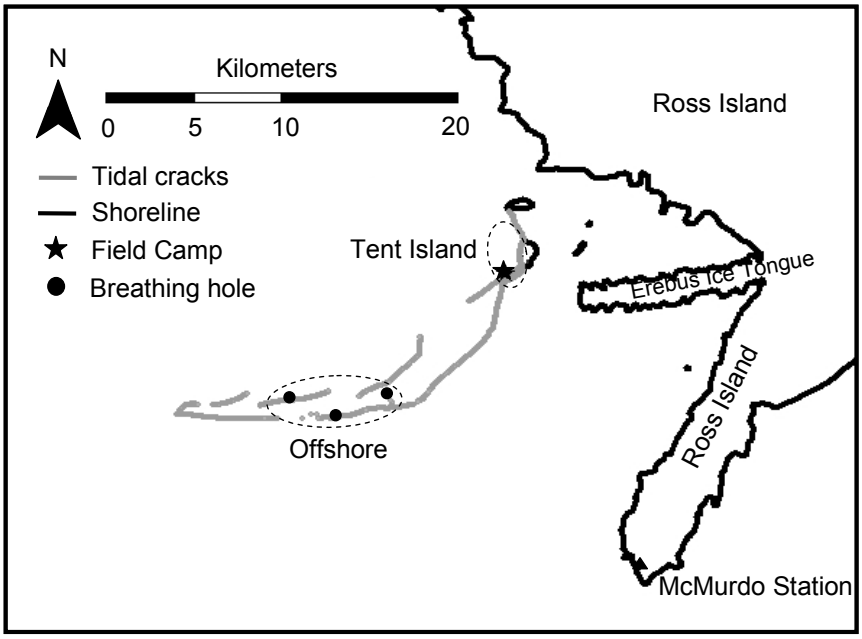


Figure 18. Representative three-dimensional dive profile from an offshore breathing hole showing foraging states: search, pursuit, attack, and handling. Inset shows details of states for a representative silverfish capture. Colors in complete dive represent different states; colors in inset represent stroking rate of the hind flippers. Each point represents the position, in three-dimensions, of a seal at 1-s intervals during the dive. Black bar at the top of figure represents both the surface of the ice and the scale of the figure in all directions.

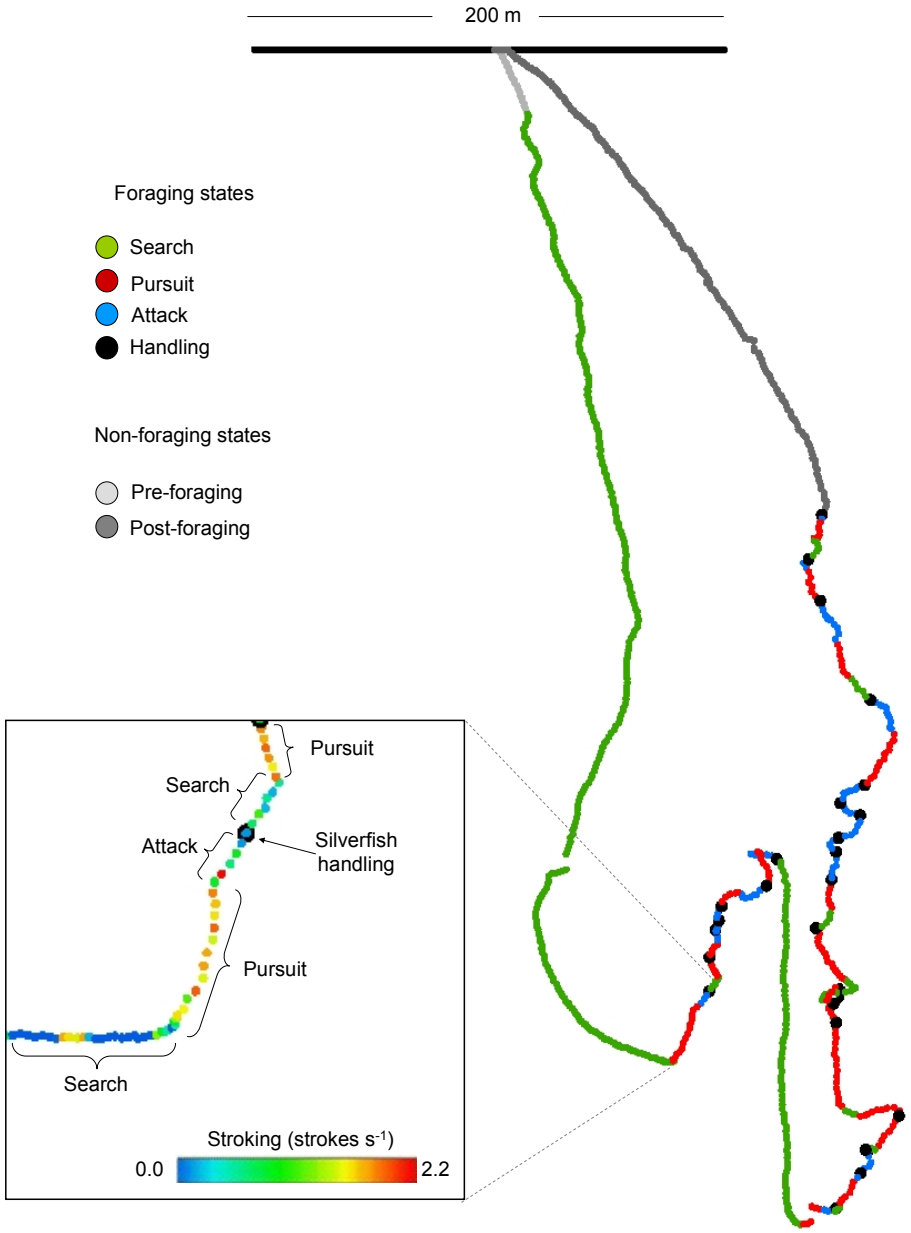


Figure 19. Percentage of *silverfish encounters* in the diet of Weddell seals foraging (a) along the coastline of Tent Island (ANOSIM, R = 0.23, P = 0.003) and (b) at offshore breathing holes (Mann-Whitney test, U = 371.5, P = 0.808). Letters above bars reflect results of pairwise comparisons. Bars that share a common letter are not significantly different (P < 0.05; Bonferroni corrected for multiple comparisons).

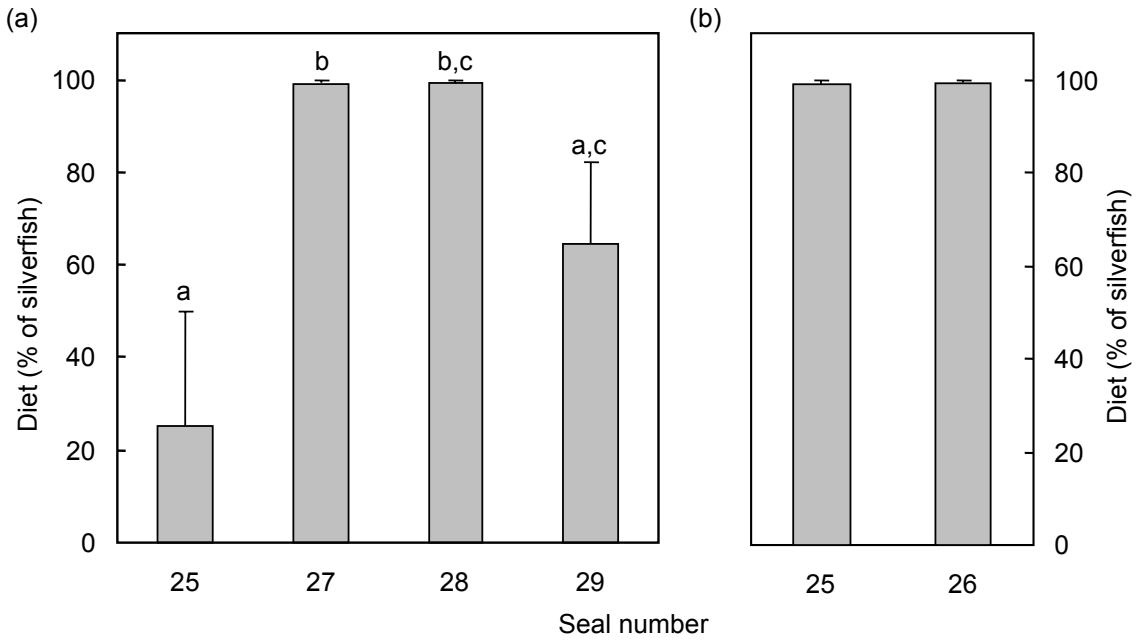


Figure 20. Relationship between average number of encounters per dive and percentage of (a) time and (b) energy spent in *attack* by seals diving at Tent Island. Slopes of regression lines for both time (ANCOVA, $F_{2,15} = 6.44$, $P = 0.01$) and energy (ANCOVA, $F_{2,15} = 6.55$, $P = 0.009$) varied among seals. Relationship between average number of encounters per dive and percentage of (c) time and (d) energy spent in *handling* by seals diving at Tent Island. Slopes of regression lines for both time (ANCOVA, $F_{2,15} = 8.23$, $P = 0.004$) and energy (ANCOVA, $F_{2,15} = 10.55$, $P = 0.001$) varied among seals.

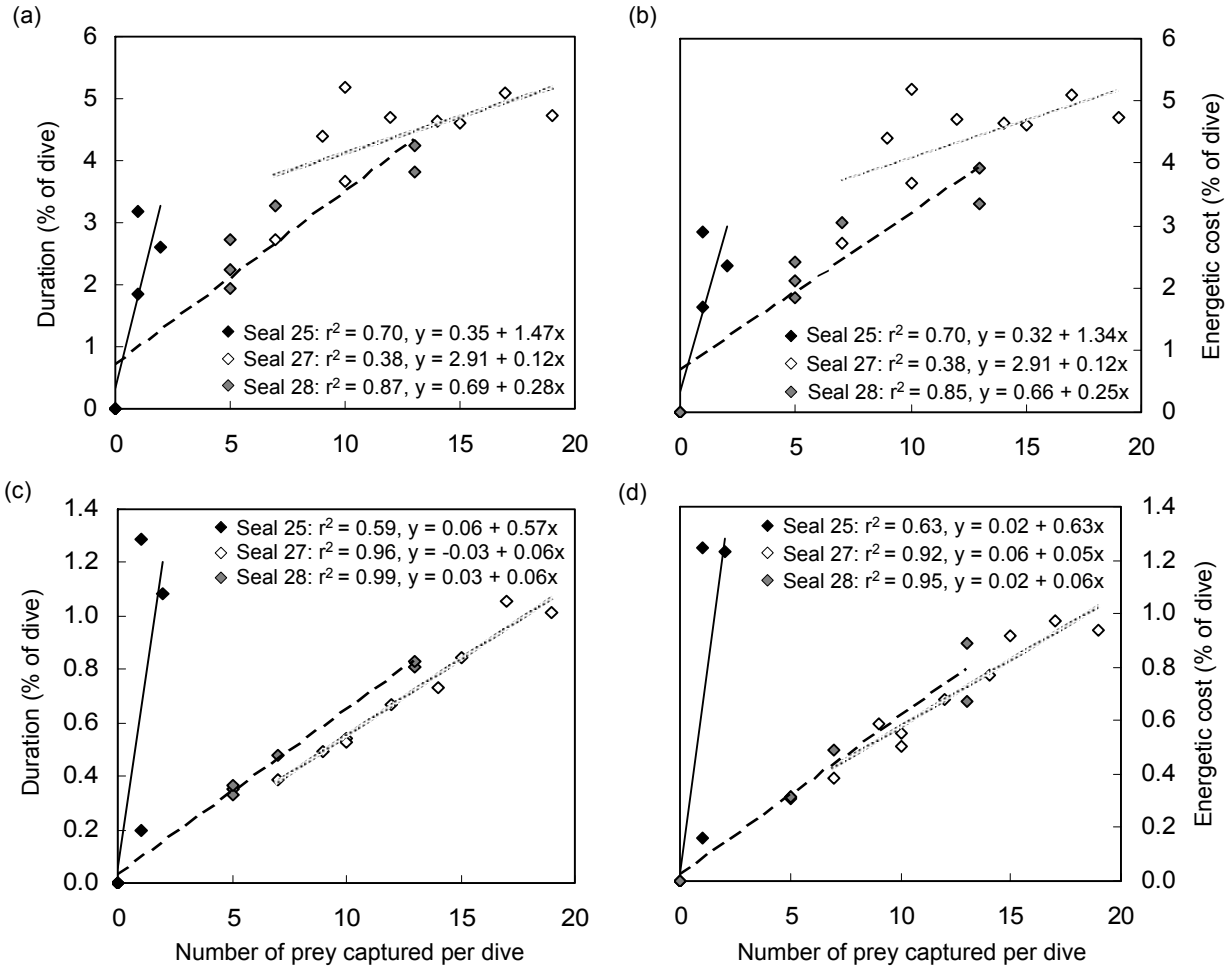


Figure 21. (a) Adjusted mean values for percentage of time spent in *search* (ANCOVA, $F_{2,15} = 2.0$, $P = 0.17$) and *pursuit* (ANCOVA, $F_{2,15} = 5.77$, $P = 0.014$) by Weddell seals diving at Tent Island. (b) Adjusted mean values for the percentage of energy spent in *search* (ANCOVA, $F_{2,15} = 1.91$, $P = 0.182$) and *pursuit* (ANCOVA, $F_{2,15} = 4.80$, $P = 0.024$). Letters above bars reflect results of pairwise comparisons. Bars that share a common letter are not significantly different ($P > 0.05$; Bonferroni corrected for multiple comparisons).

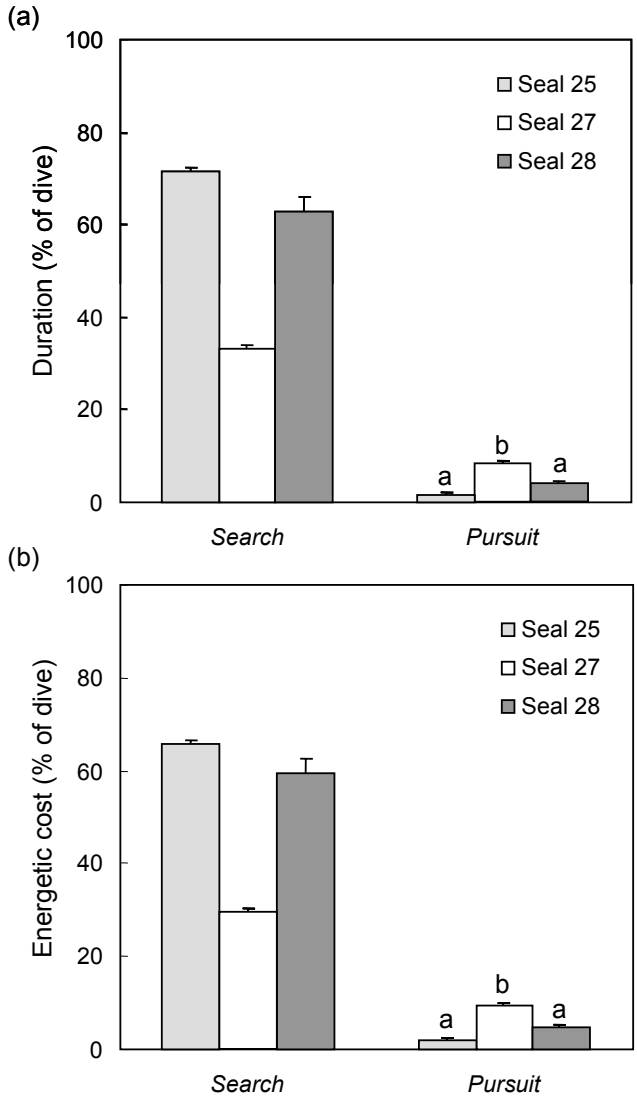
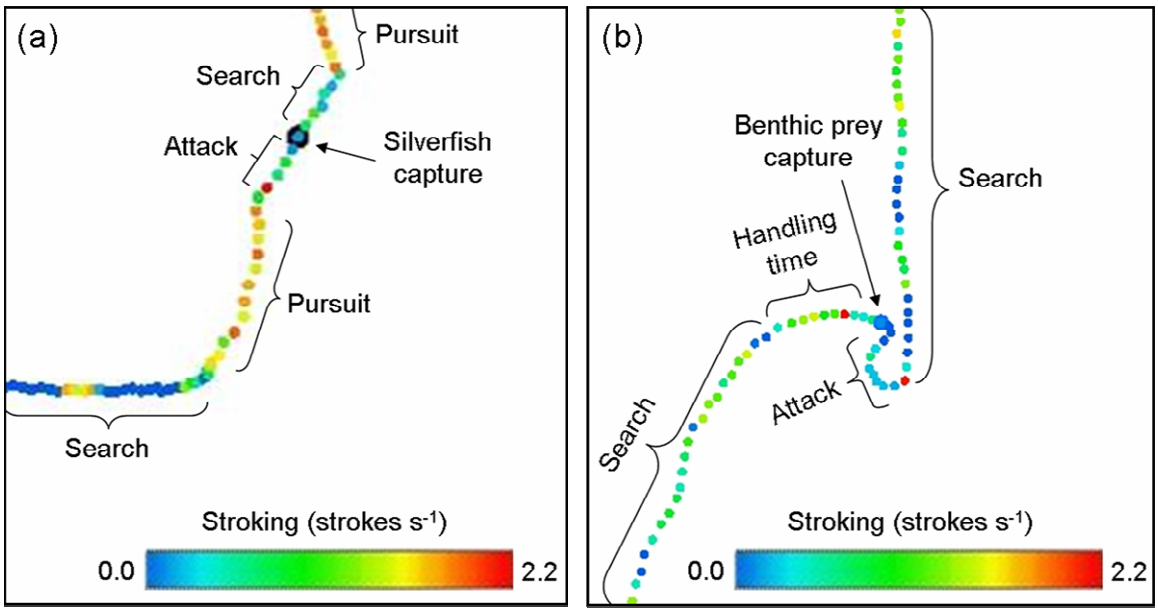


Figure 22. Three-dimensional dive paths showing the stroking pattern of foraging states (search, pursuit, attack, and handling) during (a) silverfish and (b) benthic prey encounters.



Chapter 6: Conclusions

In the studies comprising this dissertation, a video data recorder (VDR) was used to document the three-dimensional movements and prey encounters of free-ranging Weddell seals (*Leptonychotes weddellii*). The primary objective was to gain a more complete understanding of the seals' natural foraging behavior. Our results showed that free-ranging seals performed three types of foraging dives: (1) deep aerobic dives, (2) deep anaerobic dives, and (3) shallow aerobic dives. Deep aerobic dives were similar in depth and duration to the foraging dives identified in previous studies, but the shallow aerobic dives, which had been recognized by previous investigators (Schreer and Testa, 1996; Davis et al., 2003), were now found to include foraging activity. Deep anaerobic dives also differed from previous classifications and were not indicative of benthic foraging as was previously thought (Schreer and Testa, 1996).

The frequency of different types of foraging dives varied among locations within McMurdo Sound, most likely due to bathymetric differences. Deep aerobic foraging dives were more common at offshore breathing holes, an environment much like that of a previous study in which Weddell seals foraged at an isolated-hole (Fuiman et al. 2007). This provided an opportunity for a detailed comparison of foraging behavior of free-ranging seals with that of seals diving at a man-made hole. Foraging dives of free-ranging seals diving offshore were largely similar to those of seals diving at an offshore isolated-hole. However, there were differences in descent behavior (descent and meandering descent) and the frequency of several behavioral transitions. These differences appeared to be caused by a greater prey abundance of prey (Antarctic silverfish, *Pleuragramma antarcticum*) in the free-ranging study, rather than artifacts of the isolated-hole protocol. This study shows that the isolated-hole protocol does not

substantially alter foraging behavior of Weddell seals, and it provides an indication of how foraging behavior changes when prey abundance varies.

Despite efforts to select a homogenous sample of seals (with regard to sex, mass, length, geographic location), the seals displayed significant variability in foraging success and behavior. Dive depth, distance, duration, and energetic cost were important for explaining foraging success, but only under certain conditions. In shallow areas where silverfish were more difficult to reach and potentially less abundant, behavioral variability had an effect on the number of prey encountered. At Tent Island, dives that were longer, deeper, covered a greater distance, and had a higher energetic cost resulted in greater foraging success. However, this relationship was not the same for all individuals, and some seals were more successful than others, even when using the same type of behavior. Behavioral variability was not as important for explaining success when prey were more abundant and easier to access, as was the case at offshore breathing holes. Behavioral plasticity appears to be important for species that specialize on one major prey item, live in an area of variable bathymetry, and are forced to return to the surface to breathe at a distance from their prey.

Diet also varied significantly among individuals diving from breathing holes near the coastline. Two of these coastal seals specialized on silverfish, while the remaining two seals had a wider dietary breadth and consumed both silverfish and benthic prey. Although benthic prey were more accessible along the coastline than offshore, silverfish, which have a high lipid content (Clarke, 1984; Clarke and Peck, 1991; Friedrich and Hagen, 1994), also required less handling to consume. Thus, it may be more energy-efficient for seals to specialize on silverfish at the coastal location despite the additional time and energy required to travel to the depths where silverfish are located. Diet did not vary significantly among the two seals foraging at offshore breathing holes. Both seals

specialized on silverfish and spent similar time and energy searching and handling silverfish. Sample sizes were limited, but the presence of interindividual variability in diet and foraging behavior of seals hunting from breathing holes along the coastline suggests that increased effort should be made to measure the breadth of diet and foraging tactics and the energetic basis upon which foraging decisions are made by Weddell seals at these locations.

Detailed information on foraging behavior is necessary for improving our understanding of the effects of resource utilization, niche breadth (Morse, 1980), and predation pressure (Lima and Dill, 1990; Abrams, 1993) on diving marine predators. The results from this dissertation represent the most thorough understanding of the natural foraging behavior of Weddell seals to date. Results show that individual variability, prey abundance, and bathymetry cannot be ignored when describing foraging patterns and calculating energy budgets of diving predators. Ultimately, these results will improve our ability to model population- and community-level food web dynamics (Estes et al., 2003) and predict changes in the growth rates and condition of Weddell seals and other diving predators.

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Vita

Kiersten Marie Madden was born in Springfield, Missouri on February 1, 1980, the daughter of Shirley Marie Madden and Charles Theodore Madden. After completing her work at Kickapoo High School, Springfield, Missouri, in 1998, she entered Augustana College in Rock Island, Illinois. During the summers of 1999 and 2000, she worked as a teacher's aide in learning disabled and multi-handicapped classrooms for the Springfield Public School System. She also worked as an intern for the U.S. Fish and Wildlife Service in Rock Island, Illinois during the summer of 2001. In 2002, she graduated Summa cum laude and Phi Beta Kappa from Augustana College. Following the completion of her B.A., she worked as a program assistant in the Education Department at Brookfield Zoo in Illinois. In September 2002, she entered the Graduate School of The University of Texas, during which time she taught multiple laboratories of Introduction to Oceanography and worked as a Graduate Research Assistant for Dr. Lee A. Fuiman. In 2002, she was awarded the Dean's Excellence Award from The University of Texas Marine Science Department, and in 2004, she was awarded a National Science Foundation GK-12 Fellowship from The University of Texas at Austin.

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